



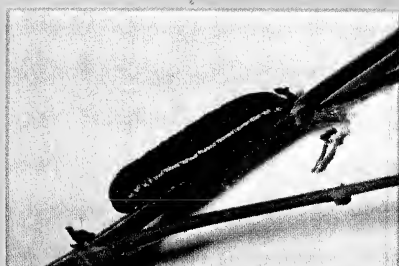
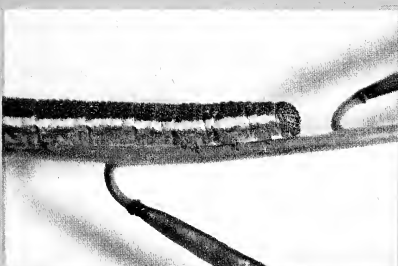
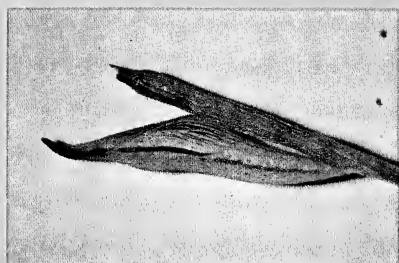
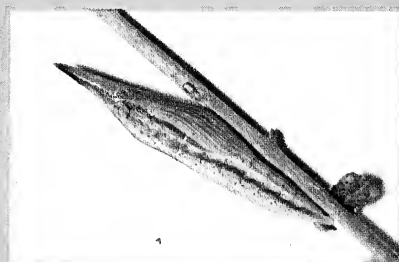
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STUDIES ON NEARCTIC *EUCHLOE*

PART 7.

COMPARATIVE LIFE HISTORIES, HOSTS AND THE MORPHOLOGY OF IMMATURE STAGES

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University of California,
Berkeley, California*

THIS PART OF THE SERIES deals with certain aspects of the life history of the Nearctic *Euchloe*. Although the "life histories" of all except *Euchloe creusa* have appeared in the literature, no comparisons have been made. This study emphasized the immature stages, important differences in oviposition sites, larval behavior, larval color patterns, larval setation, and pupal configuration.

LIFE HISTORY

Host. — All *Euchloe* oviposit and feed upon maturing plants of the family Cruciferae. The food plants utilized are the result of selection by ovipositing females.

Among the species of Cruciferae which occur at any locality, female *Euchloe* may select more than one species as suitable hosts, but never appear to utilize all of them. Those species selected must have had several prior requirements. These are: (1) the plant should grow in full sunlight, (2) the plant should be more than five inches in height with an erect configuration, and (3) the clusters of unopened flower buds should be terminal and tightly clustered (except some *Euchloe hyantis* hosts).

The role of allyl isothiocyanate levels in determining the suitability of various crucifers as hosts for *Euchloe* is unknown.

The groups of hosts used by most, well-observed species are broad. Qualitative differences in host utilization are pronounced

only between the two species groups. The three members of the "Ausonides group," i.e. *Euchloe ausonides*, *E. creusa*, and *E. olympia*, tend to utilize species of *Arabis* and "mustard-like" crucifers, i.e. *Arabis glabra*, *Barbarea*, *Brassica*, and *Sisymbrium*, while the "Hyantis group," i.e. *Euchloe hyantis*, tends to utilize *Caulanthus*, *Descurainia*, and *Streptanthus* with greater frequency.

That host specificity levels within the Cruciferae are broad is shown by the frequent utilization of introduced species of the family. Swales (1966) briefly discusses the range extension of some pierids due to the introduction of crucifers into disturbed areas around villages in Arctic Canada. Opler (1969) explained the role of introduced species of *Brassica* as a possible factor permitting the facultative bivoltinism of *Euchloe ausonides* in coastal central California.

All pertinent locality and host data for all Nearctic *Euchloe* are summarized in Table 1.

Oviposition site. — Members of the "Ausonides group" almost always place their eggs on unopened flower buds of the host. This behavioral feature has been reported for *E. ausonides* by Coolidge and Newcomer (1908) and Remington (1952), while Shull (1907) and Meiners (1938) reported the same pattern for *E. olympia*. I have observed many hundreds of eggs of *E. ausonides* and only rarely were eggs found anywhere but on unopened buds. Eggs of *Euchloe creusa* near Banff were all found on unopened flower buds of *Draba lanceolata*.

Although *Euchloe hyantis* females may select flower buds as oviposition sites, other portions of the plant are utilized with greater frequency. Coolidge (1925) reported that eggs of *Euchloe hyantis lotta* were found on flower buds, leaves, or the stems of host plants. Near El Portal, Mariposa County, California, I observed that the eggs of *Euchloe hyantis* were most frequently placed on the lower surface of the saggitate clasping leaves of *Streptanthus polygaloides*.

Larval behavior. — Upon emerging from the egg, larvae of *Euchloe* seek unopened flower buds upon which to feed. J. A. Scott, Division of Entomology, University of California, Berkeley, (Personal communication) states that first instar larvae of *Euchloe ausonides* die if fresh unopened buds are not available. Upon hatching, larvae of *E. hyantis*, emerging from eggs laid on leaves or stems of the host, must find the reproductive portions of the plant soon after hatching. To do this the larvae make

TABLE I.
HOST AND LOCALITY DATA FOR VARIOUS SPECIES OF EUCHLOE

Euchloe ausonides

Arabis drummondi Gray

Canada, Ontario, Geraldton Forest (Thunder Bay District), 28 June 1966. J.C.E. Riotte. Jour. Lepid. Soc., 22(1): 41 (1968).
Colorado, Boulder County, Nederland 6 July 1949. C.L. Remington. Psyche, 59(2):63 (1952).
Colorado, Gunnison County, Gothic, 9600', 10 July 1967, J. Emmel and O. Shields. J. Res. Lepid., 8(1):31 (1970).

Arabis fendleri (Wats.) Greene var. spatifolia (Rydb.) Rollins
Colorado, Boulder County, Nederland, 6 July 1949, CL. Remington. Psyche, 59(2):63(1952).

Arabis glabra (L.) Berh.

Colorado, Boulder County, Spring Gulch, 7 July 1949, C.L. Remington. Psyche, 59(2):62 (1952).
California, Contra Costa County, Berkeley Hills, NE Oakland, 3 June 1963 J.A. Powell. Preserved larvae in California Insect Survey.

Barbarea vulgaris (L.)

California, Contra Costa County, Russelmann Park, Mt. Diablo, 24 April 1966, P.A. Opler. Personal observation.

Brassica campestris L.

California, Contra Costa County, Briones Regional Park, 28 March 1970, P.A. Opler. Personal observation.

Brassica kaber (D.C.)

California, Alameda County, Strawberry Canyon, 18 April 1964, P.A. Opler. Personal observation.
California, Contra Costa County, Briones Hills Regional Park, 28 March 1970, P.A. Opler. Personal observation.
California, Contra Costa County, Tilden Regional Park, 18 April 1968, P.A. Opler. Personal observation.
California, Santa Clara County, Alum Rock Park, 28 February 1964, P.A. Opler. Personal observation.

Brassica nigra (L.) Koch

California, Alameda County, Strawberry Canyon, 10, 15 April 1970, P.A. Opler. Personal observation.
California, Contra Costa County, Pt. Richmond, 18 April 1969, J.A. Scott. (preserved larvae).
California, Santa Clara County, New Almaden, 4 May 1964, P.A. Opler. Personal observation.

Descurainia Californica (Gray) Shultz

Colorado, Gunnison County, Schofield Pass, 10,400', 14, 18 July 1967, J. Emmel and O. Shields. J. Res. Lepid., 8(1):31 (1970).

Erysimum capitatum (Dougl.) Greene

Colorado, Boulder County, Nederland, 6 July 1949, C.L. Remington.
Psyche, 59(2):63 (1952).

Isatis tinctoria L.

California, Modoc County, Buck Creek Ranger Station, 11 June 1970, P.A. Opler. Personal observation.

Raphanus sativa L.

California, Contra Costa County, Briones Regional Park, 28 March 1970, P.A. Opler. Personal observation.

Sisymbrium altissimum L.

Colorado, Boulder County, Boulder Canyon, 6500', Mt. Flagstaff,
Nederland, 8-9 July 1949, C.L. Remington. Psyche, 59(2):62 (1952).

Euchloe creusaDraba lanceolata Royle

Canada, Alberta, Moraine Lake, 6800', Banff National Park, 27
June 1965, P.A. Opler. Personal observation.

Euchloe olympiaArabis drummondii Gray

Michigan, Montcalm County, T12N, R10W, Sec. 19, 20 June 1966,
M.C. Nielsen. Preserved larvae in Michigan State University Collection.
Michigan, Roscommon County, T24N, R1W, Sec. 3. 5 July 1967,
M.C. Nielsen. Preserved larvae in Michigan State University collection.

Arabis lyrata L.

Indiana, Lake Michigan dunes between Clarke Junction and Pine,
C.A. Shull. Ent. News, 18(3): 73 (1907).
Michigan, Berrien County, T53, R19W, Sec. 29, 29 May, 3-5 June
1967, M.C. Nielsen. Preserved larvae in Michigan State University
Collection.

Arabis missouriensis Greene

Missouri, St. Louis County, Ranken, 28 April 1935, E.P. Meiners,
Proc. Missouri Acad. Sci., 4:154-156 (1938).

Sisymbrium sp.

West Virginia, 1891, W.H. Edwards, Butterflies of North America.

Euchloe hyantisArabis glabra (L.) Bernh.

California, Sierra County, Shenanigan Flat, 14 miles W Downieville,
15 May 1970, P.A. Opler. Personal observation.

Arabis holloelii var. pinetorum (Tides.) Roll.

California, San Bernardino County, Sugarloaf Peak, 8000', July
1970, W. Hovanitz. J. Res. Lepid., 8(1): 17 (1970).

Caulanthus amplexicaulis Wats.

California, Kern County, between Mojave and Randsburg, Coolidge.
Ent. News, 19:204-210 (1925).

Caulanthus crassicaulis (Torr.) S. Wats.

California, Modoc County, 5 miles S Ft. Bidwell, 11 June 1970, P.A. Opler.
Personal observation.

Descurainia pinnata (Walt.) Britton

California, San Bernardino County, Newberry Mountains, 3/4 mile
NW Kane Spring Road, 27 March 1964, J.F. and T.C. Emmel. Letter
of 24 November 1964.
California, San Bernardino County, Phelan, J.A. Comstock and C.M.
Dammers, Bull. So. Calif. Acad. Sci., 31(2): 35-37 (1937).

Descurainia pinnata var. nelsonii (Rydb.) Detl.

Washington, Benton County, Vernita, 6 April 1966, E.J. New comer.
Letter of 20 May 1967.

Isatis tinctoria L.

California, Modoc County, Buck Creek Ranger Station, 11 June 1970, P.A.
Opler. Personal observation.

Sisymbrium altissimum L.

Washington, Benton County, Vernita, 22 April 1967, E.J. Newcomer.
Letter of 20 May 1967.

Stanleya pinnata (Pursh) Britton

California, Inyo County, Wildrose Station, Panamint Mountains,
15 May 1969, P.A. Opler. Personal observation.

Streptanthella longirostris (Wats.) Rydb.

California, San Bernardino County, Phelan, J.A. Comstock and
C.M. Dammers. Bull. So. Calif. Acad. Sci., 31(2): 35-37 (1935).

Streptanthus bernardinus (Greene) Parish

California, San Bernardino County, Lake Arrowhead, 5000', 29 June
1966, C. Henne. Letter of 7 July 1966.

Streptanthus polygaloides Gray

California, Mariposa County, 2 miles W El Portal, 12 April 1964,
P.A. Opler. Personal observation.

Streptanthus tortuosus Kell.

California, Sierra County, Shenanigan Flat, 14 miles W Downieville,
15 May 1970, P.A. Opler. Personal observation.

Streptanthus sp.

California, Alpine County, Hope Valley, 9 July 1949, J.W. MacSwain,
Preserved larvae in California Insect Survey.
California, Siskiyou County, Little Castle Lake, 20 July 1969,
P.A. Opler. Personal observation.
California, Tuolumne County, Lodgepole Campground, Sonora Pass,
2 July 1966, P.A. Opler. Personal observation.

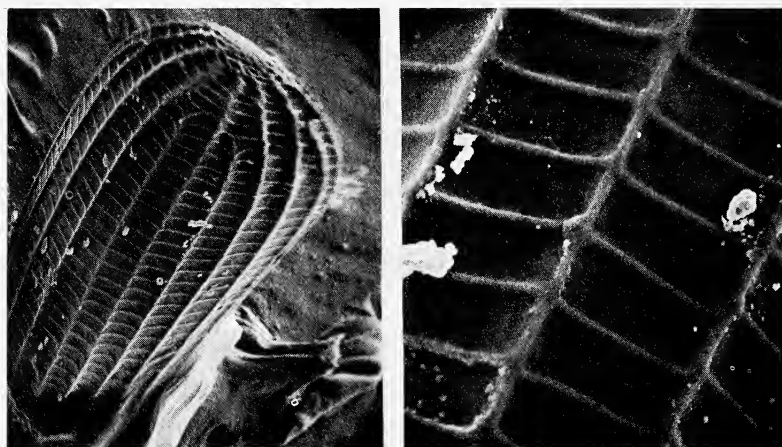


Fig. 1.

Left, egg of *Euchloe ausonides*, 100 X. Strawberry Canyon, Alameda Co., Calif.; right, same, 500 X. Stereoscan electron photomicrographs by Wayne Steele.

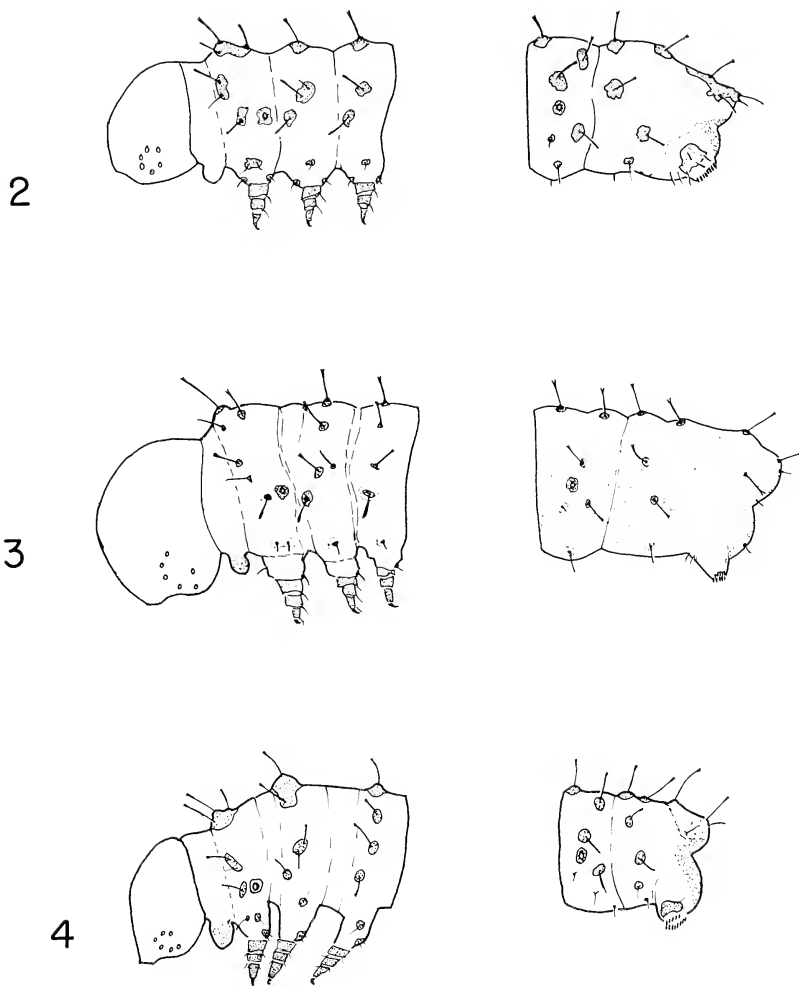
geo-negative or photo-positive movements. On *Streptanthus polygaloides* young larvae of *Euchloe hyantis* bore through the clasping leaves lying between the site of oviposition and flowering portions of the plant. During this movement the larvae do not pause to feed on leaf material.

Young larvae of *Euchloe* feed upon unopened flower buds and flowers. During this period the larvae are comparatively hidden. The young larvae of *E. ausonides* station themselves vertically amongst the flower cluster and always cover the portion of the plant upon which they rest with loosely spun silk.

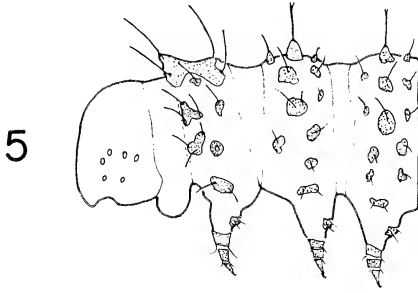
The first instar larvae of *Euchloe hyantis* were found to have another anomolous habit which seems to be an adaptation to feeding upon *Streptanthus*. The calyx of *Streptanthus* flowers is almost closed distally. In order to reach the inside of the calyx the young larva bores a small hole through the side of the calyx, enters, and feeds upon the flower from within.

Older larvae feed in more exposed positions and include the seed pods in their diet. While feeding upon seed pods the larvae orient with their anterior end directed toward the apical end of the pods.

Pupation. — The final stages of ecdysis which lead directly to pupation in *Euchloe* seem to occur in a characteristic manner that holds true for all species of *Euchloe*, and probably take place in much the same fashion for all members of the tribe Euchloini. When the larva has finished feeding it commences a search for a suitable pupation site which is usually located on the food plant. Upon finding a pupation site the larva attaches itself by means of a caudal button of silk and silk girdle with the anterior portion at a higher elevation than the posterior. Pupation then takes place between 24 and 72 hours later. At a time varying from just prior to the wandering phase to a time subsequent to being stationed in the pupation position, the larva becomes purplish in color. A quantitative lack of observations prevents the determination of the specificity of any of the above phenomenon. The appropriate passages from the literature upon which the above narration was based are cited below. Shull (1907), in regard to the mature larva of *Euchloe olympia*, said "Shortly a purplish tinge makes its appearance at the posterior end and about the thorax. The color gradually extends anteriorally until the whole body shows it. This change immediately precedes and accompanies the wandering of the larva seeking a place to pupate."

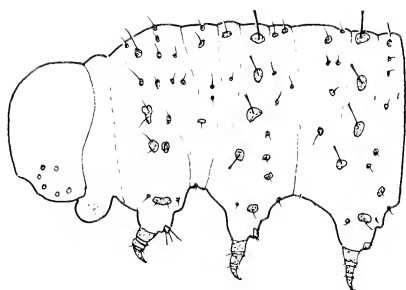


First instar larvae, segments T 1-3, A 9-10. Fig. 2, *Euchloe ausonides*, Alum Rock Park, Santa Clara Co., Calif.; Fig. 3, *Euchloe creusa*, Moraine Lake, Banff National Park, Alberta, Canada; Fig. 4, *Euchloe olympia*, Berrien Co., Mich.

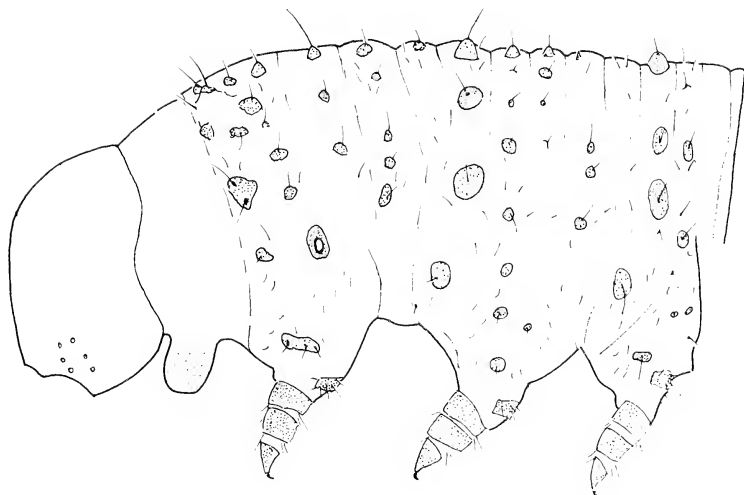


Second instar larvae, segments T 1-3, A 9-10. Fig. 5, *Euchloe ausonides*, Buck Creek Ranger Station, Modoc Co., Calif.; Fig. 6, *Euchloe olympia*, Montcalm Co., Mich.

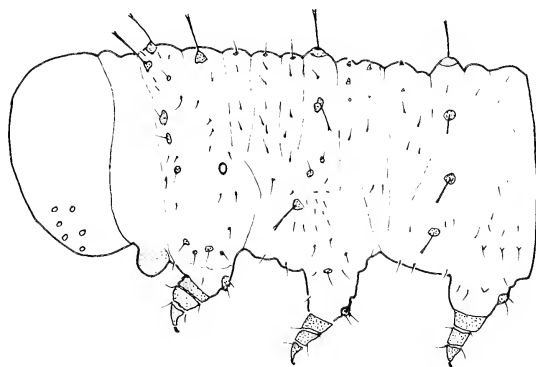
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Third instar larvae, segments T 1-3, A 9-10. Fig. 7, *Euchloe ausonides*, Buck Creek Ranger Station, Modoc Co., Calif.; Fig. 8, *Euchloe olympia*, Montcalm Co., Mich.; Fig. 9, *Euchloe hyantis*, Buck Creek Ranger Station, Modoc Co., Calif.

Mead (1877) described the pupation of *Euchloe hyantis* based upon observation of larvae collected in Yosemite Valley, Mariposa County, California, as follows, "Just before the change to chrysalis the caterpillar turns dull purple. The chrysalis retains this color for a day or two and then gradually assumes a waxy grayish white color." Coolidge (1925) noted that the larva of *Euchloe hyantis lotta* "becomes solid purplish red" just prior to pupation. Comstock and Dammers (1932), while describing the larvae of *Euchloe hyantis lotta*, stated that "a short time prior to pupation they turn a mottled dark maroon over the dorsal and lateral surface above the stigmatal line. Pupation occurs on the food plant as in *Anthocharis cethura*." (i.e. with a girdle, caudal button, and the head pointing upward, *vide* Comstock and Dammers).

MORPHOLOGY OF IMMATURE STAGES

Egg. The eggs are typical of Euchloini in being columnar with the micropylar area broadly rounded. The eggs have from 15-20 prominent vertical ridges which are interconnected by less prominent horizontal ridges (Fig. 1.).

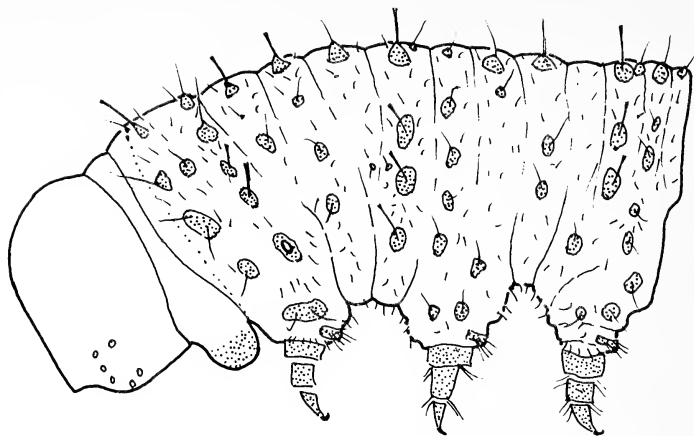
The eggs undergo a series of progressive color changes as the embryo develops. Coolidge and Newcomer (1908), while describing the life history of *Euchloe ausonides*, stated that the "color when first laid (was) light bluish green changing in 24-30 hours to light orange. By the third day the color is almost vermilion, and about the sixth day the egg turns dirty yellow brown, especially so apically."

Larva. — The larvae of *Euchloe* differ interspecifically and interstadially in features of color and setation. These differences will be systematically discussed below.

The sequence of color changes undergone by the larvae of *Euchloe ausonides* (Coolidge and Newcomer, 1908) and *Euchloe olympia* (Shull, 1907) is parallel.

The first instar larva is orange-yellow with a black head, while the second instar larva is greenish with a black head. Markings typical of the final three instars are discernible on the third instar larva: a gray-green dorsal stripe, yellow-green subdorsal stripes, gray-green supraspiracular stripes, yellow spiracular stripes, and subspiracular and ventral areas green. The head of the third instar larva is green-black. The fourth instar larva of the two species has the same markings, but the head capsule

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11



Fourth instar larvae, segments T 1-3, A 9-10. Fig. 10, *Euchloe ausonides*, Buck Creek Ranger Station, Modoc Co., Calif.; Fig. 11, *Euchloe olympia*, Montcalm Co., Mich.

is greenish gray. The spiracular stripe of the fifth instar larva is white and is subtended with pale yellow. Plate 1, figs. 1, 6.

Larvae of *Euchloe hyantis* undergo a similar series of changes, but have a different color pattern. The color pattern of the last three instar larvae is distinctive. The dorsal area is green (occasionally with a narrow purplish line). The subdorsal area is also green, while the supraspiracular area is purplish. The spiracular area is white or yellow. The subspiracular and ventral areas are green. The head capsule is green. Interpopulation variation of larval color pattern in *Euchloe hyantis* was noticed, while larval coloration of *Euchloe ausonides* and *E. olympia* varies within very narrow limits. Plate 1, figs. 3, 5.

The spiracular stripe is white in most populations of *Euchloe hyantis*, but may be yellow in some populations in the western foothills of the Sierra Nevada. The color of the dorsal and subdorsal areas is also variable. In most populations (Vernita, Wash.; cismontane Calif.) these areas are green, while these areas are grayish in some Great Basin populations (John Emmel, 1117 9th St., Apt. 207, Santa Monica, Ca. 90403, per. com.) and yellowish-green in the San Bernardino Mountains population (Chris Henne, P. O. Box 1, Pearblossom, Calif., personal communication).

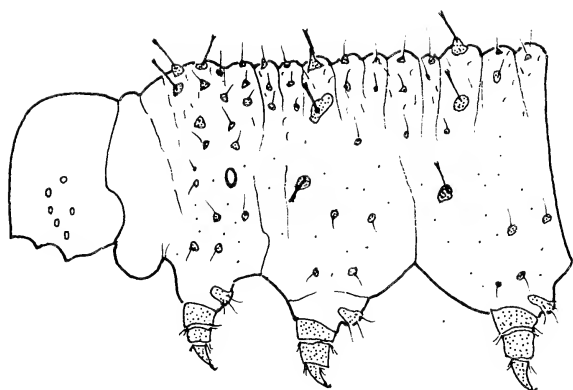
Chaetotaxic line drawings of *Euchloe* larvae are presented as figures 2-15. These drawings portray the three thoracic segments for all larvae as well as the eighth and ninth abdominal segments for first instar larvae. The microscopic primary setae (Hinton, 1946) are not necessarily portrayed.

Certain primary setae on the dorsal, subdorsal, and lateral areas are thickened and may be cleft at their apices. Coolidge (1925) reported that the setae of *Euchloe hyantis* supported "hyaline drops of fluid," while Shull (1907) reported that the setae of *Euchloe olympia* were glandular. If the forked setae do exude secretions, it would be of extreme interest to know what is their function and composition.

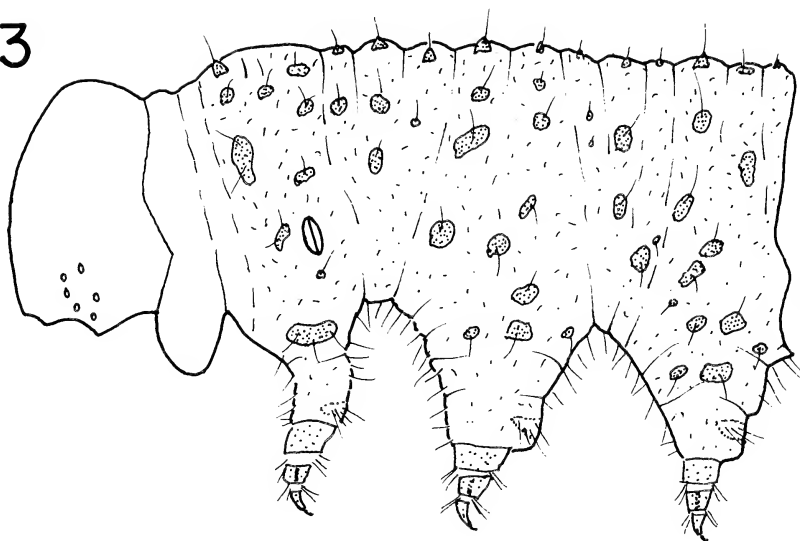
Prothoracic segment setae XD1, D2, XD2, SD1, SD2, and L1, mesothoracic setae D1, D2, SD1, SD2, and L1 are thickened and cleft in the *Euchloe* larvae.

The subdorsal group of primary setae on the prothoracic segment occurs on the same sclerotized chalaza for almost all larvae of the "Ausonides group," but occur on separate chalazae on *Euchloe hyantis* larvae.

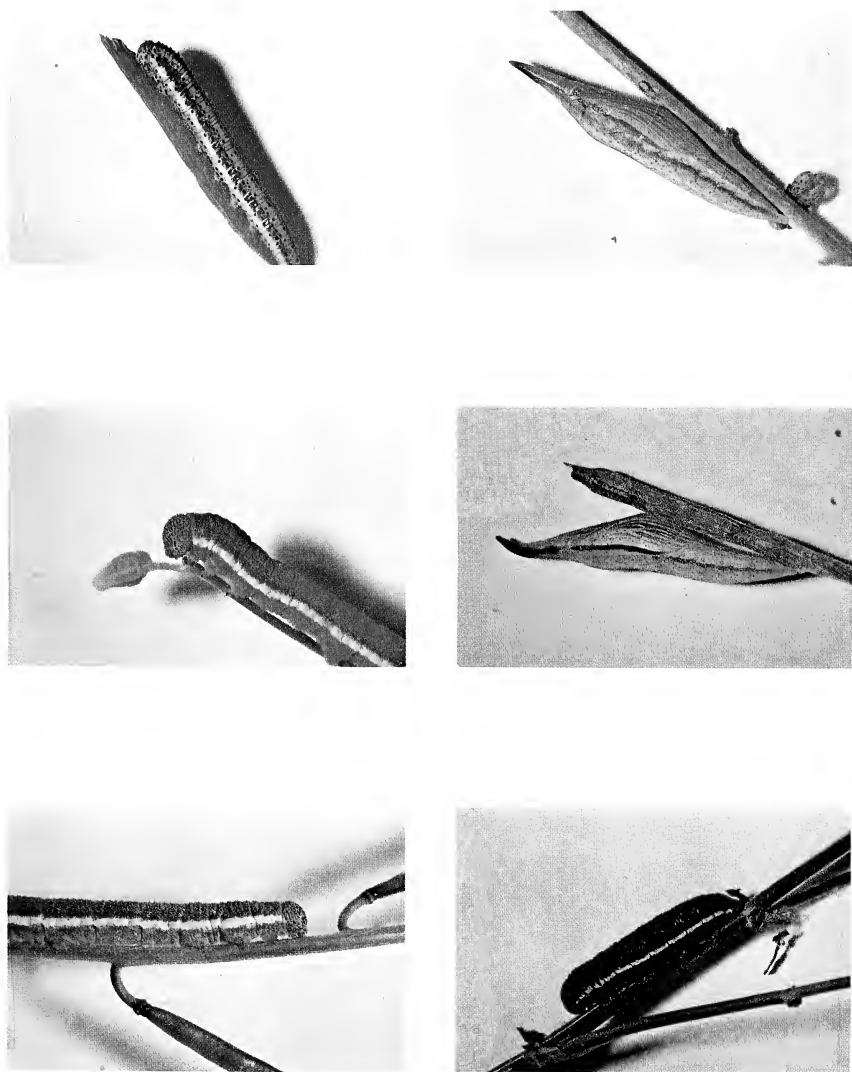
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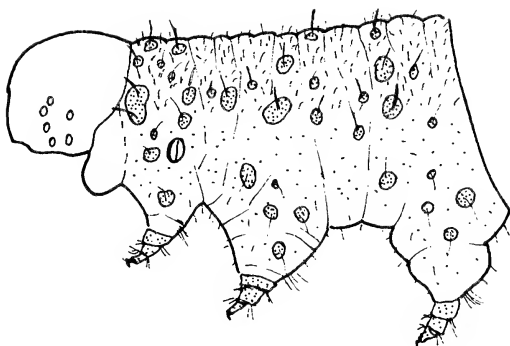
Fourth instar larvae, segments T 1-3, A 9-10. Fig. 12, *Euchloe hyantis*, Buck Creek Ranger Station, Modoc Co., Calif. Fifth instar larvae, segments T 1-3, A 9-10, Fig. 13, *Euchloe ausonides*, Buck Creek Ranger Station, Modoc Co., Calif.



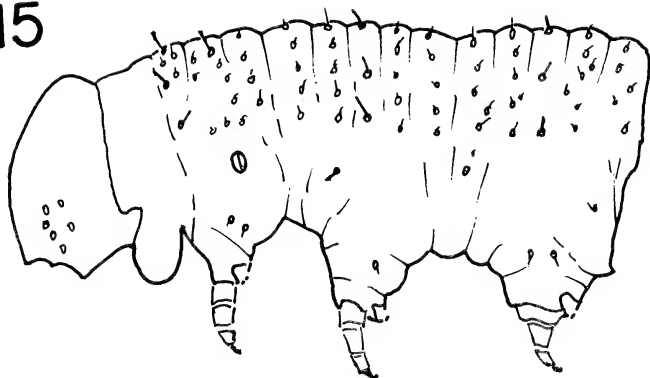
Color Plate 1.

1. *Euchloe ausonides*, 5th instar, Briones Regional Park, Contra Costa Co., Calif.;
2. *Euchloe ausonides*, pupa, Briones Regional Park, Contra Costa Co., Calif.;
3. *Euchloe hyantis*, 5th instar, Shenanigan Flat, Sierra Co., Calif.;
4. *Euchloe hyantis*, pupa, Shenanigan Flat, Sierra Co., Calif.;
5. *Euchloe hyantis*, 5th instar, near Fallon, Nevada, collected by J. F. Emmel;
6. *Euchloe hyantis*, prepupa, Shenanigan Flat, Sierra Co., Calif. (upside down).

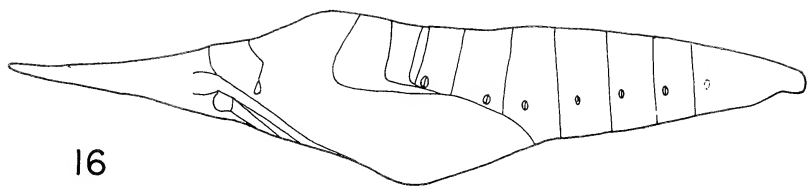
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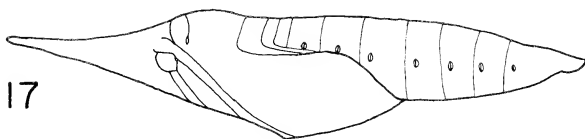
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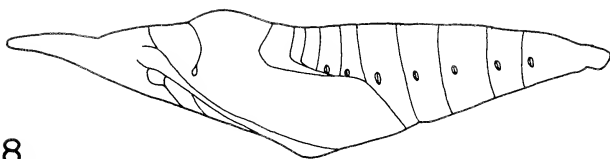
Fifth instar larvae, segments T 1-3, A 9-10. Fig. 14. *Euchloe olympia*, Roscommon Co., Mich.; Fig. 15, *Euchloe hyantis*, Buck Creek Ranger Station, Modoc Co., Calif.



16



17



18

Pupae, lateral aspect. Fig. 16, *Euchloe ausonides*, Strawberry Canyon, Alameda Co., Calif.; Fig. 17, *Euchloe olympia*, Montcalm Co., Mich.; Fig. 18, *Euchloe hyantis*, El Portal, Mariposa Co., Calif.

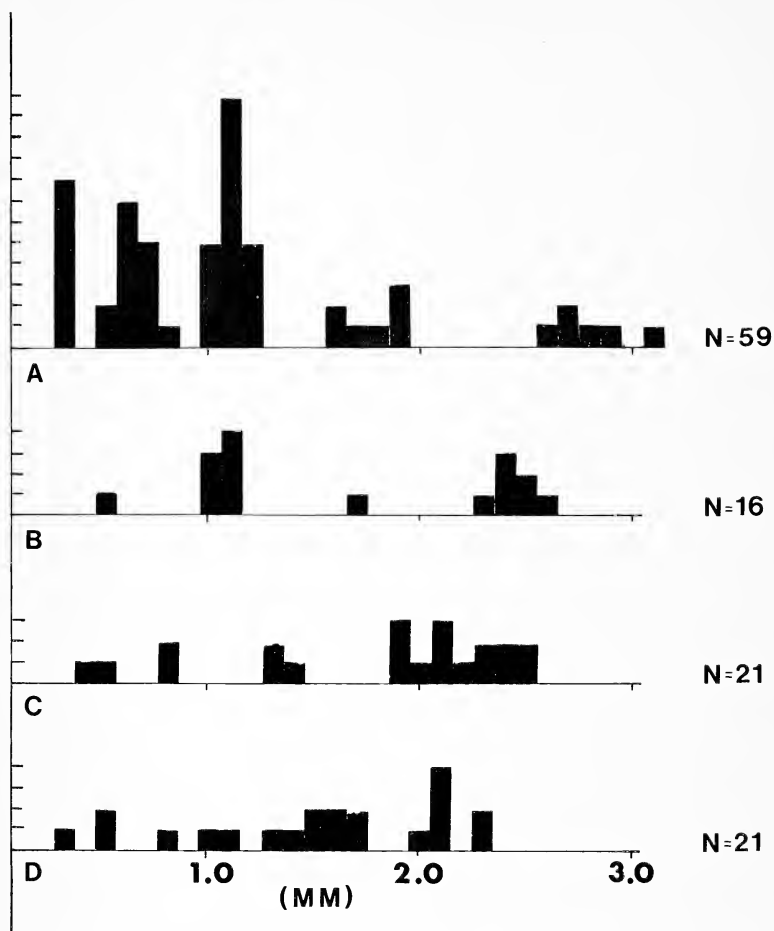


Fig. 19—Bar graph of larval head capsule widths. A. *Euchloe ausonides*, San Francisco Bay area (Alameda, Contra Costa, and Santa Clara Counties); B. *Euchloe ausonides*, Buck Creek Ranger Station, Modoc Co., Calif.; C. *Euchloe olympia*, Michigan; D. *Euchloe hyantis*, California (Mariposa, Modoc, and Sierra Counties).

The successive instars of each *Euchloe* species display distinct trends in setal coloration and size. With each successive instar, size of primary setae becomes greater on *Euchloe ausonides* larvae, remains about the same on *Euchloe olympia* larvae, and becomes smaller on *Euchloe hyantis* larvae.

On first instar *Euchloe* larvae all primary setae are melanized. Ultimate instar larvae have dorsal and subdorsal primary setae darkened and the primary setae of lateral, subventral, and ventral areas demelanized.

The secondary setae which appear on *Euchloe* larvae in increasing numbers on successive instars also vary in size and prominence. The length of secondary setae becomes longer on larvae of *Euchloe olympia*, remains about the same on larvae of *Euchloe ausonides*, and become shorter on larvae of *Euchloe hyantis*.

The apparent color of secondary setae on ultimate instar larvae is uniformly pale on *Euchloe ausonides* larvae, and dark on dorsal and subdorsal areas of *Euchloe olympia* and *Euchloe hyantis* larvae.

The extent and melanization of the sclerotized setiferous chalazae and pinaculi also differs between species and successive instars of the same species. The sclerotized chalazae of *Euchloe ausonides* and *Euchloe olympia* larvae become greater in extent with each succeeding instar, remaining about the same proportion to larval size. The chalazae of *Euchloe hyantis* larvae become progressively smaller with each succeeding instar, paralleling the size decrease of the primary setae.

The sclerotized chalazae or pinaculi bearing primary setae are darkened on all areas of all instars of *Euchloe* larvae, with the exception of lateral areas on ultimate instar larvae of *Euchloe hyantis*.

The bases of secondary setae on all ultimate instar larvae are darkened on dorsal and subdorsal areas and pale on the lateral areas. On the subventral and ventral areas they are darkened on *Euchloe ausonides* and *Euchloe hyantis*, while most are pale on *Euchloe olympia* larvae.

Pupa. — Pupal marking and coloration is extremely variable. Some idea of the pupal coloration may be seen by referring to Plate 1, figs. 2 and 4.

Although the recurvature of *Euchloe* pupae is somewhat variable, the relative proportions of the pupae are slightly differentiated. Line drawings of the pupae (Figs. 16-18) show that the ratio of the cephalic portion to pupal length is greater

for *Euchloe ausonides* (.28) than for *Euchloe olympia* (.25) and *Euchloe hyantis* (.24). The dorsal surface of the cephalic portion of *Euchloe hyantis* pupae is slightly emarginate when viewed laterally.

SUMMARY

Certain features of the life history and morphology of the immature stages of *Euchloe* emphasize the division of the Nearctic members into two species groups. In particular, location of oviposition site, larval behavior, larval color pattern and chaetotaxy are characters whose condition in the two species groups indicates genetic isolation of long standing.

ACKNOWLEDGMENTS

The following individuals provided information or material representing the immature stages of *Euchloe* which proved invaluable in the construction of this paper: J. F. Emmel, Idyllwild, California; T. C. Emmel, Gainesville, Florida; Chris Henne, Pearblossom, California; E. J. Newcomer, Yakima, Washington; M. C. Nielsen, Lansing, Michigan; and Fred Thorne, El Cajon, California. Roland Fisher, Michigan State University, East Lansing, Michigan, kindly loaned larval material representing *Euchloe olympia*.

I am indebted to Wayne Steele, Livermore, California, for his preparation and provision of scanning electron photomicrographs of the egg of *Euchloe ausonides*.

Evert Schlinger, Division of Entomology, University of California, Berkeley, reviewed the manuscript of this paper and provided suggestions and corrections which were incorporated into the final draft.

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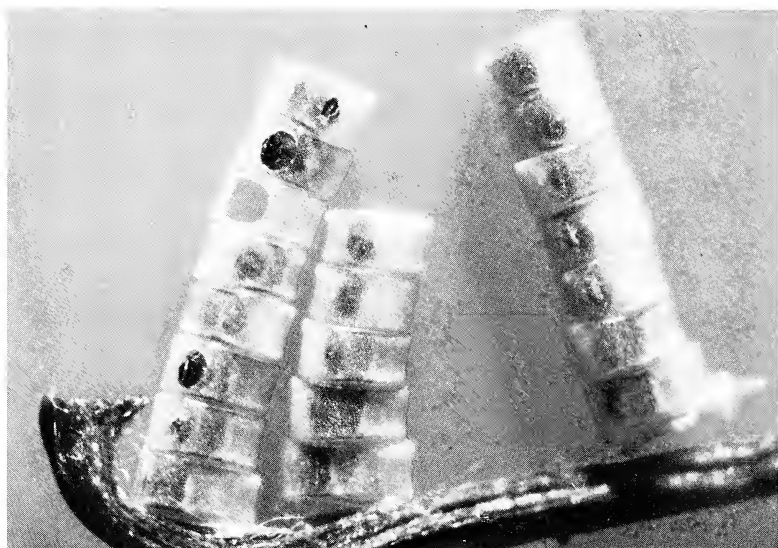
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3 STACKS OF THE EGGS OF
HEMISTOLA
HATCHING

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Eggs of *Hemistola chrysoprasaria* (Esper) (*GEOMETRIDAE-GEOMETRINAE*) (det. F. Benz), SHOWING LARVAE IN THE PROCESS OF EMERGING: These eggs were kindly given to me by Dr. F. Benz of Binningen, Switzerland, who obtained them from a female taken at mv. light, 26 JUNE 1968, at Ober-Zeihen AG, Switzerland. (The eggs were deposited 28 JUNE 68, and hatching took place 10 days later). The mode of oviposition, in precise stacks, is characteristic. Perhaps the procryptic value of these stacks lies in the way they simulate the appearance of tightly-coiled immature tendrils on the stems of the foodplant (*Clematis vitalba* L. - *RANUNCULACEAE*)? The photograph was made when the larvae were just in the process of chewing their way to freedom. The third one down from the top (in the left stack) had already gone, leaving the (characteristic) *clean-cut* exit-hole in the end of its empty egg shell. The second one down (same stack) had nearly finished its exit-hole; the dark-colored object filling the hole is the head of the young larva. The top egg (same stack) shows a very small hole just being started. In the other 2 stacks can be seen the (dark) larval heads, aligned in rows, still inside the eggs. The egg dimensions for this series were: 0.90-0.85 x 0.65 x 0.40 mm. (N. McFarland photo; species code-number Gm. 195).



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AN ANNOTATED CHECKLIST OF
THE MACROHETEROCERA OF
SOUTH-EASTERN ONTARIO

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INTRODUCTION

PROGRESS IN THEORETICAL ECOLOGY, community evolution and basic pollution research is seriously retarded by the absence of systematically collected, carefully documented population samples of sufficient size in both number of individuals and in species number. This is especially true for the animal kingdom.

Lepidoptera, especially night flying ones, are an admirably suitable taxocene for such research. Yet, even here, few collections are adequate in sampling technique, quantification and consistency, making it very difficult to use these collections for the formulation of generalizations concerning ecosystem or community structure.

In the past several years we have been conducting an intensive complete-season collecting program in an attempt to survey the macroheterocera fauna of the Kingston region. This forms part of a broader study on the effects of environmental disturbance on species diversity, and the evolution of community structure, the results of which will be published elsewhere. In this publication we wish to record the moth species collected, their flight periods and relative abundance, and notes on their life histories.

The list covers the south-eastern portion of southern Ontario, an approximately triangular area bordered by 75° 45'W longitude, 45° 00'N latitude, and the St. Lawrence River System (figure 1). This is a physiographically diverse area, with variably overlain Paleozoic sediments interrupted in the center of the

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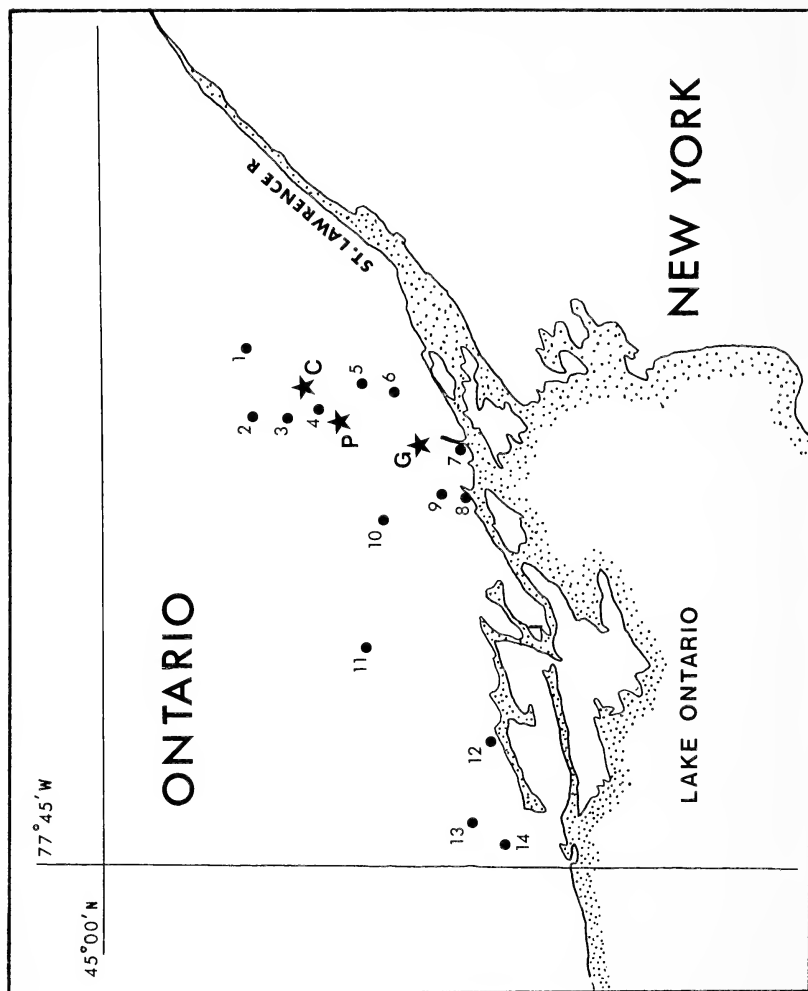


Fig. 1.—South-eastern Ontario, with the principal collecting sites G, P, and C. The fourteen other localities are as follows: 1) Portland, Leeds Co., 2) Westport, Leeds Co., 3) Bedford Mills, Frontenac Co., 4) Lake Opinicon, Frontenac Co., 5) Cranberry Lake, Frontenac Co., 6) Washburn, Frontenac Co., 7) Kingston, Frontenac Co., 8) Amherstview, Lennox & Addington Co., 9) Westbrook, Frontenac Co., 10) Harrowsmith, Frontenac Co., 11) Marlbank, Hastings Co., 12) Belleville, Hastings Co., 13) Frankford, Hastings Co., and 14) Wooler, Northumberland Co.

region by a protrusion of the Precambrian Shield. The predominant forest of white pine and northern hardwoods contains a considerable infusion of austral (Carolinian) elements (Snyder *et al.*, 1941; Soper, 1962; Harmsen, Hebert and Ward, 1974). Much of the original vegetation has been replaced by second growth forest and agricultural land.

The macroheterocera fauna of the area exhibits a remarkable species richness which coincides with a great regional diversity of plants (Beschel *et al.*, 1970) and birds (Quilliam, 1973). The south-eastern Ontario total of 820 + macroheteroceran species may be compared to Ferguson's (1955) listing of 764 species from the entire province of Nova Scotia and Moore's (1955) tabulation of 1006 species from the state of Michigan. Single-locality species totals for south-eastern Ontario (see below) are far in excess of those normally reported in the literature for temperate regions (e.g. Preston, 1948; Williams, 1964; McFarland, 1965; LaFrance, 1968).

METHODS

The bulk of the records is based on daily collections of nocturnal macrolepidoptera made by the authors over at least one complete collecting season (spring to autumn) at each of three collecting sites: Glenburnie, Perth Road and Chaffey's Locks, hereafter designated G, P, and C respectively (Table 1). The former is located in marginal agricultural land on Ordovician limestone, while P and C are situated in areas of mixed forest on Precambrian metamorphic rock. All specimens were collected with a 20-watt blacklight (GE FT20T12-BL) set against a white cloth background. The light was run all night and moths were collected off the screen at dawn.

We consider one complete sample of the fauna to consist of all macroheterocera collected over an entire season at one light. Thus site G was sampled once, C and P each four times. Altogether 101,862 individuals comprising 778 species were identified and recorded. The total numbers of species recorded in this manner from each collecting site are 427 (G), 571 (C), and 701 (P).

Additional material from G, C, and P was obtained by rearing immature stages, collecting diurnally, and collecting with light and bait outside the prescribed collecting schedule. Sporadic collecting has also been carried out at 14 other localities in

south-eastern Ontario (Figure 1). Most of these collections were made by the authors but some records from the Royal Ontario Museum, Toronto (ROM) (mostly collected by J.C.E. Riotte) and the Canadian National Collection, Ottawa (CNC) have also been included. These additional data bring the total number of recorded species to 822.

The majority of the material was identified by P.S.W. and P.D.N.H., utilizing particularly Forbes (1948, 1954, 1960), Ferguson (1955), McGuffin (1967, 1972), and access to the Canadian National Collection, Ottawa. Some difficult material was determined by specialists mentioned in the acknowledgements.

The families, genera, and species are arranged alphabetically, and subspecies names are not used. Nomenclature essentially follows McDunnough (1939), in conjunction with recent revisionary changes. Authors names have been omitted since all species names may be found in McDunnough (1938) or Forbes (1948, 1954) with the exception of the following: *Anisota finlaysoni* Riotte (1969); *Eupithecia rindgei* McDunnough (1949), *Semiothisa marmorata* Ferguson (1972), *Semiothisa pinostrobata* Ferguson (1972), *Semiothisa signaria* (Hübner) (= *S. dispuncta* (Walker)). *Thera juniperata* (Linnaeus) (= *T. procteri* Brower), *Helicoverpa zea* (Boddie) (= *H. obsoleta* of authors, not Fabricius), and *Hypenodes palustris* Ferguson (1954).

THE CHECKLIST

In the following list, the numbers in parentheses after G, C, or P refer to the total numbers of individuals collected at each site under the prescribed collecting schedule. This gives a rough idea of relative abundances, but it is worth remembering that G was only sampled one year. If a species was only recorded from G, C, or P outside the collecting program this is indicated by a dash in parentheses. Records from the fourteen other collecting localities are usually only included if less than half a dozen individuals have been collected at G, C, and P.

AGARISTIDAE

Allypia octomaculata

C(-), P(-). Adults diurnal, May 10-Jun 26;
reared from larvae on Vitis riparia

ARCTIIDAE

Apantesis anna

C(18), P(130). Jun 8-Jul 9.

Apantesis arge

G(20), C(5), P(4). May 8-14; Jul 23-Sep 6.
Predominantly in late summer.

Apantesis celia

G(1), C(-), P(28). May 31-Jun 24.

Apantesis nais

C(58), P(228). May 21-Jul 14; Aug 19.

Apantesis parthenice

G(3), C(2), P(19). Aug 10-Sep 8.

Apantesis phalerata

G(65), C(-). Jun 2-17; Aug 6-Sep 7; Oct 13.

Apantesis phyllira

G(2). Aug 5-Sep 5.

Apantesis virgo

G(7), C(2), P(6). Jul 19-Aug 3.

Apantesis virguncula

G(29), C(-), P(17). Jun 13-Jul 27.

Arctia caxa

C(-), P(1). Aug 7. Two specimens at light at
C: Aug 18, 1964; Aug 10, 1966.

Cisthene plumbea

C(-). Two specimens at light: Jul 14, 1963;
Jul 17, 1967.

Clemensia albata

G(2), C(5), P(4). Jun 26-Jul 28.

Crambidia casta

C(-). One specimen at light: Aug 23, 1969.

Crambidia pallida

C(10), P(168). Jul 27-Sep 4.

Crambidia pura

G(22), P(1). Jun 12-26; Aug 6-31.

Cynia tenera

G(10), C(24), P(71). Jun 2-Jul 30.

Estigmene acraea

G(103), C(9), P(51). May 24-Sep 4. Probably
bivoltine.

Euchaetias egle

G(32), C(22), P(29). Jun 4-Aug 2.

Euchaetias oregonensis

G(4), C(12), P(21). May 31-Jul 13; Jul 16-Aug 9.

Halysidota caryae

G(20), C(19), P(300). May 24-Jul 11.

Halysidota maculata

Belleville. Aug 10, 1962. (Carleton University
Collection).

Halysidota tessellaris

G(75), C(374), P(2734). Jun 3-Aug 27.

Haploa confusa

G(47), C(20), P(57). Jul 19-Aug 18.

Haploa contigua

G(1), C(11), P(3). Jul 15-28.

Haploa lecontei

C(1), P(14). Jun 17-Jul 23.

Holomelina aurantiaca

C(9), P(58). Jun 18; Jul 6-Aug 23.

Holomelina ferruginosa

G(154), C(50), P(50). Jun 2-Jul 10; Jul 7-Sep 6.

Holomelina opella

C(18), P(158). Jun 23-Aug 29.

Hyphantria cunea

G(118), C(19), P(192). Jun 1-Jul 21.

Hypoprepia fucosa

G(20), C(137), P(832). Jul 9-Sep 13.

Hypoprepia miniata

G(3), C(17), P(505). Jul 13-Sep 15.

Lycomorpha pholus

C(-), P(3). Jul 14-Aug 10. Common diurnal
species, frequently visiting Solidago flowers,
Jul 29-Aug 22.

Phragmatobia assimilans

G(3), C(22), P(168). May 2-Jun 3.

Phragmatobia fuliginosa

G(68), C(12), P(55). May 17-Jun 7; Jul 20-
Sep 15. Second brood larger.

Pyrrharctia isabella

G(73), C(83), P(165). May 31-Aug 6; Aug 26-
Sep 12.

Spilosoma congruum

G(1), C(181), P(186). May 14-Jul 4; Aug 22.

Spilosoma primum

G(3), C(45), P(115). May 7-Jun 29.

Spilosoma virginicum

G(252), C(230), P(463). May 1-Sep 16; Oct 22.
Several overlapping generations.

Trigrioides bicolor

P(10). Jul 24-Aug 6.

CITHERONIIDAE

Anisota finlaysoni

Kingston: Jun 27, 1969 (12) (ROM); Otter Lake,
Frontenac Co.: Jul 6, 1974 (12). Eggs and
larvae collected on Quercus in vicinity of
Belleville.

Anisota rubicunda

C(297), P(1463). May 19-Jul 29; Aug 17-Sep 10.

Anisota virginienensis

C(4), P(29). May 30-Jul 17. Only females at
light; males diurnal.

Eacles imperialis

C(43), P(76). Jun 12-Aug 8.

DREPANIDAE

Drepana arcuata

G(2), C(309), P(636). May 4-Jul 10; Jul 3-
Aug 30.

Drepana bilineata

G(1), C(91), P(353). May 2-Jun 28; Jul 5-Sep 5.

Eudelina herminiata

C(1), P(3). May 31-Jun 12; Aug 12. Locally
common in hardwood swamps at P. Jun 7-16.

Oreta rosea

G(1), C(13), P(65). Jun 8-Jul 21; Jul 30-
Sep 15.

EPIPLEMIDAE

Callizia amorata

C(3), P(1). May 31-Jun 29.

EUCHROMIIDAE

- Ciseps fulvicollis* G(96), C(5), P(41). Jun 9-Jul 11; Jul 17-Sep 8; Oct 11.
Ctenucha virginica G(243), C(25), P(45). Jun 1-Aug 5; Sep 15.

GEOMETRIDAE

- Abbottana clemataria* G(2), C(154), P(92). May 1-Jun 24.
Aethalura anticaria C(64), P(33). May 7-Jun 26.
Alsophila pometaria G(83), C(-), P(4). Apr 8-May 7; Nov 4.
 Common, diurnal spring species in Kingston, Mar 21-May 1. Fewer adults emerge in the autumn.
Anacamptodes ephyraria C(42), P(108). Jun 25-Aug 10.
Anacamptodes vellivolata G(75), C(18), P(40). May 2-Jul 4; Jul 14-Aug 10; Sep 4-23.
Anagoga occiduaris C(1), P(25). May 4-Jun 14.
Anavitrinella pampinaria G(186), C(28), P(80). May 15-Jul 8; Jul 15-Sep 8.
Antepione thisoaria P(32). May 23-Jun 25.
Apicia confusaria G(15), C(6), P(57). Jul 6-Aug 6.
Bapta glomeraria P(2). May 8.
Bapta semiclarata C(-), P(1). May 14. Collected during the day at C, P, and Harrowsmith. May 17-29.
Bapta vestaliata G(16), C(16), P(89). May 17-Jun 28; Jul 17.
Besma endropiaria C(2), P(33). May 30-Jul 15.
Besma quercivoraria G(9), P(85). May 11-Jul 10; Jul 27-Aug 21.
Biston cognataria G(34), C(39), P(115). May 20-Aug 26. Frequency of melanic specimens in 1971 at P was 12/73 or 16.4%.
Brephos infans C(-), P(-). Diurnal, early spring species, Apr 11-May 9.
Campaea perlata G(12), C(136), P(303). Jun 2-Jul 29; Aug 15-Sep 15.
Caripeta angustiorata G(1), C(22), P(43). Jul 15-Aug 15.
Caripeta divisata C(2), P(2). Jul 19-Aug 1.
Caripeta piniata G(2), C(42), P(179). May 30-Jul 31.
Catopyrrha coloraria Wooler. May 9, 1972 (4cc, 298), flushed from Ceanothus.
Cepphis armataria G(1), P(1). Jun 10; Aug 14.
Cepphis decoloraria C(2). Jun 6-18.
Chlorochlamys chloroleucaria G(34), C(24), P(35). May 25-Jul 17; Jul 25-Aug 31.
Cingilia catenaria C(5), P(859). Sep 10-Oct 2. Larvae collected on Myrica gale and on ericaceous bog plants; in outbreak proportions on sphagnum bogs at Harrowsmith and Westport in 1973.
Cleora projecta P(3). May 8-Jun 17. Also reared from larvae on Myrica gale in small sphagnum bog at F.
Cleora sublunaria P(1). May 19.
Coryphista meadi G(6), C(-), P(1). Aug 9-Sep 13. Larvae on Berberis vulgaris at C. Also attacks ornamental Berberis in urban areas, including Kingston.
Cosymbia pendulinaria G(1), C(64), P(227). May 14-Sep 14. Two, partially overlapping broods with peaks in mid-June and early August.
Deileinea erythremaria G(1), C(2), P(21). May 29-Jul 2; Jul 26-Aug 30.
Deileinea variolaria G(5), C(22), P(57). Jun 8-Jul 15; Jul 13-Sep 3.
Diactinia silaceata C(6). May 25-Jun 2; Jul 29-Aug 12.
Dichorda irridaria C(13), P(27). May 19-Jun 22; Jul 31-Aug 17.
Drepanulatrix liberaria C(4). Sep 6-Oct 12.
Dyspteris abortivaria C(1), P(1). Jun 2-15.
Dysstroma hersiliata G(1), C(7), P(19). Jun 17-Jul 20.
Dysstroma sp. Bedford Mills, Westport. Two specimens at light in sphagnum bogs, Jun 23-29, 1973.
Earophila vasaliata G(1), C(4), P(22). Apr 20-May 30.
Ectropis crepuscularia G(9), C(60), P(92). May 1-Jun 16; Jun 16-Aug 16.
Ematurga atomaria P(-). Harrowsmith, Westport. Diurnal bog species, May 24-Jun 26.
Ennomos magnarius G(53), C(63), P(367). Jul 28-Oct 22.
Ennomos subsignarius G(10), C(134), P(246). Jul 6-Aug 20.
Epirrhantis substriataria Wooler. One specimen at light: May 9, 1972.
Epirrhoe alternata C(1), P(18). Jun 2-29; Aug 6-Sep 9.
Epirrita autumnata C(45), P(18). Oct 5-24.
Erannis tiliaria G(47), C(30), P(47). Oct 8-Nov 4.
Euchlaena effecta G(2), C(4), P(10). Jun 27-Jul 26.
Euchlaena irraria C(1), P(24). Jun 2-Jul 6.
Euchlaena johnsonaria G(3), C(2), P(39). Jul 6-Aug 10.

- Euchlaena marginaria* C(6), P(25). May 14-Jun 20.
Euchlaena obtusaria G(1), C(5), P(2). Jun 2-30.
Euchlaena serrata G(31), C(10), P(7). Jul 9-Aug 5.
Eudule mendica C(1), P(8). Jul 6-Aug 5.
Eufidonia discospilata C(-). Harrowsmith, Westport. Diurnal species, common in bogs, May 24-Jul 8.
Eufidonia notatoria C(5), P(47). May 19-Jul 2.
Eugonobapta nivosa G(2), C(33), P(189). Jul 2-Aug 8.
Eumacaria latiferrugata G(5), P(4). Jun 6-18; Jul 4-Aug 5.
Euphyia centrostrigaria G(9), C(14), P(34). Jun 24-Oct 22. Apparently two or more generations, commonest in August - October. Possibly a migratory species.
Euphyia multifera P(3). Jun 7-20.
Euphyia unangulata G(46), C(19), P(25). May 16-Jul 13; Aug 2-Sep 19.
Eupithecia affinata C(2), P(9). Aug 9-Sep 3.
Eupithecia castigiata C(1). Jun 13.
Eupithecia coloradensis P(1). Jun 16.
Eupithecia coagulata P(6). Aug 15-27.
Eupithecia columbiata C(31), P(244). May 1-Jun 11.
Eupithecia filmata P(4). May 7-19.
Eupithecia fletcherata P(146). Aug 8-Sep 2.
Eupithecia fumosa G(5), C(4), P(27). May 9-Jun 22; Aug 3-Sep 4.
Eupithecia gibsonata C(19), P(23). May 7-Jun 28.
Eupithecia luteata P(5). Jun 10-26.
Eupithecia miserulata G(13), C(12), P(45). May 1-Jul 1; Aug 3-Nov 3. Much commoner in autumn; possibly overwinters as adult.
Eupithecia misturata C(1), P(1). May 8; Jul 17.
Eupithecia mutata P(3). Jun 30-Jul 5.
Eupithecia palpata G(1), C(24), P(89). May 14-Jun 27.
Eupithecia perfusca P(6). Jun 17-27; Jul 27.
Eupithecia ravocostaliata G(2), C(6), P(14). May 1-Jun 29.
Eupithecia rindgei P(1). Jun 2.
Eupithecia russellata P(3). Jun 26-29.
Eupithecia satyrata C(1). Aug 25.
Eupithecia sheppardata C(1), P(2). May 29-Jun 19.
Eupithecia sobrinata G(14), C(27), P(77). Aug 14-Oct 13. Larvae collected on Juniperus communis.
Eupithecia stratonata G(1), C(3), P(13). May 19-Jun 19.
Eupithecia swetti P(2). May 16-18.
Eustroma nubilata G(2). Jul 10-Aug 1.
Guenaria basilaria G(1), C(3), P(6). Jun 22-Aug 5.
Haematopsis grataria G(51), C(1), P(2). Jun 11-15; Jul 23-Sep 16. Second generation much more prevalent.
Heliomata cycladata C(1). Jun 14. One other record from C: Jun 14, 1967.
Hesperumia sulphuraria C(-). Two specimens at light: Jul 9-12, 1967.
Hethemia pistaciaria G(3), C(69), P(79). May 10-Jun 26.
Heterophleps triguttaria C(-), P(1). Jul 27. Collected diurnally at C: Jul 30, 1969.
Homochlodes fritillaria G(1), P(15). Jun 3-Jul 8.
Horisme intestinata G(1), C(39), P(10). May 21-Jul 1; Jul 14-Aug 24.
Hydrelia albifera P(4). May 30-Jun 17; Aug 13.
Hydria undulata G(1), C(-), P(28). Jun 1-Aug 21.
Hydriomena divisaria C(1). May 3.
Hydriomena renunciatia C(13), P(58). May 7-Jun 15; Jul 12-26.
Hypagyrtis piniata C(14), P(46). Jun 9-Jul 30.
Hypagyrtis subatomaria C(1), P(108). Jun 9-Jul 28; Aug 27.
Hyperetis alienaria C(36), P(247). May 8-Jun 26; Jul 30-Aug 6. Only three second generation individuals.
Isturgia truncataria P(-). Harrowsmith, Westport. Common diurnal bog species, May 6-Jun 26.
Itame andersoni complex C(5), P(83). Jun 9-Jul 26. Reared from larvae collected on Ribes and Vaccinium.
Itame brunneata P(1). Jun 26. Common in sphagnum bog at Westport, Jun 26-27, 1973.
Itame exhauspicata C(6), P(30). Jun 7-Jul 14.
Itame pustularia G(5), C(59), P(536). Jun 30-Sep 4.
Itame ribearia G(3), C(-), P(8). Jul 18-30. Larvae collected on a cultivated Ribes sp.
Itame subcessaria C(5), P(44). Jul 6-Aug 1.
Itame sulphurea P(-). Bedford Mills, Portland. Adults diurnal in sphagnum bogs, the males occasionally at light, Jun 11-Jul 29. Also reared from larvae collected on Myrica gale.
Lambdina fiscellaria C(6), P(3). Sep 3-Oct 5.
Lobophora nivigerata G(2), C(42), P(108). May 5-Jun 28; Jul 10; Jul 23.
Lozogramma subaequaria C(1), P(29). May 8-Jun 11.

- Lycia ursaria*
Lygris diversilineata
Lygris explanata
Lygris serrataria
Lygris testata
Lytrosia unitaria
Melanolophia canadaria
Melanolophia signataria
Mesoleuca ruficollata
Mesotheta incertata

Metanema determinata
Metanema inatomaria
Metarranthis duaria
Metarranthis hypochraria
Metarranthis indeclinata
Metarranthis obfirmaria

Metarranthis refractaria
Metarranthis warneri
Nematocampa filamentaria

Nemoria bistriaria

Nemoria mimosaria
Nepytia canosaria
Nyctobia atroliturata
Nyctobia limitaria
Operophtera bruceata

Orthofidonia flavivenata
Orthofidonia tinctaria
Palaecrita vernata
Percnopylota obtipata

Perizoma basaliata
Pero honestarius

Pero marmorata
Pero morrisonarius
Phaeoura quernaria
Phigalia olivacearia

Phigalia titea

Plagodis alcoolaria
Plagodis nigrescens

Plagodis phlogosoria

Plagodis serinaria
Pleurogrypha insularia

Prochoerodes transversata
Protitame virginalis
Protocharmia porcellaria
Rheumaptera hastata
Scopula cacuminaria
Scopula enucleata
Scopula inductata

Scopula junctaria
Scopula persimilis

Selenia alciphearia
Semiothisa aemulataria
Semiothisa bicolorata
Semiothisa bisignata
Semiothisa gnophosaria
Semiothisa marmorata
Semiothisa mellistrigata
Semiothisa minorata
Semiothisa neptaria
Semiothisa ocellinata
Semiothisa orillata
Semiothisa oweni
Semiothisa pinostrobata
Semiothisa sexmaculata
- G(8), C(5), P(157). Apr 12-Jun 5.
 G(32), C(40), P(38). Jul 9-Sep 15. Includes form gracilineata. Reared from larvae on Vitis.
 C(20), P(77). Jun 30-Aug 14; Sep 23.
 G(1), P(6). Jul 9-27.
 C(1), P(2). Sep 14-30.
 G(2), C(19), P(30). Jun 24-Jul 19.
 C(4), P(18). May 29-Jun 23.
 G(2), C(21), P(22). May 4-Jun 24.
 C(2), P(2). May 21-Jun 7; Aug 9-13.
 C(-), P(-). Harrowsmith, Washburn, westport, Portland. Adults diurnal, on bogs and dry heaths, Apr 26-Jun 2.
 C(-). One specimen at light: May 23, 1973.
 C(43), P(117). May 14-Jul 6; Jul 14-Aug 25.
 G(5), C(3), P(22). May 4-Jun 18.
 C(2), P(7). May 21-Jun 10.
 G(1), C(12), P(36). May 24-Jun 23.
 C(-), P(1). Jun 7. Adults normally diurnal, on dry heaths or bogs at C, P, and Westport, May 10-Jun 5.
 G(1), C(13), P(19). May 31-Jun 20.
 G(3), C(1), P(11). Jun 10-29.
 G(4), C(20), P(45). Jul 3-Aug 3. Includes three of form chagnoni from P.
 G(10), C(170), P(750). May 1-Jun 17; Jul 9-Aug 17; Sep 15.
 C(12), P(13). May 28-Jun 19; Oct 27.
 G(4), C(26), P(4). Aug 8-Sep 26.
 C(-), P(30). Apr. 19-May 19.
 G(1), C(12), P(15). May 3-28.
 G(4), C(-), P(-). Nov 2-3. Common late fall species at C (Oct 31-Nov 8).
 C(7), P(188). May 1-29.
 P(1). Jun 9.
 G(66), C(20), P(28). Apr 8-May 29.
 G(47), C(9), P(36). May 18-Nov 3. Commonest in September and October; possibly migratory.
 C(1). Jul 20.
 G(820), C(41), P(83). May 10-Jul 4; Jul 26-Oct 11.
 P(2). Aug 11-12.
 C(7), P(2). May 31-Jun 25.
 G(1), C(1), P(11). May 23-Jun 30.
 G(4), C(7), P(70). Apr. 12-May 19. All males, no melanics.
 G(38), C(31), P(118). Apr 12-May 27. All males; frequency of melanic specimens in 1971 at P was 5/100 or 5.0%.
 C(38), P(152). May 8-Jun 18.
 C(-), P(1). Jun 10. One specimen at light at C: Jun 20, 1973.
 G(2), C(174), P(1476). May 1-Jun 25; Jul 5-Aug 14.
 C(26), P(100). May 10-Jun 17.
 G(21), C(55), P(36). May 31-Oct 25. Apparently several overlapping generations.
 G(1), C(53), P(136). Jul 29-Sep 15.
 G(1), C(8), P(368). May 8-Jul 16; Jul 23-Sep 4.
 C(6), P(9). Jun 27-Jul 23.
 C(-). One specimen at light: Jul 1, 1973.
 G(7), C(1), P(-). Jul 4-Aug 14.
 G(11), C(55), P(260). Jun 29-Aug 19.
 G(70), C(27), P(8). May 31-Jul 17; Aug 4-Sep 14.
 P(1). Jun 18.
 G(-). One male reared from mature wandering larva collected Apr 6, 1970.
 P(1). May 8.
 C(-), P(57). May 29-Jun 29; Jul 24-Sep 2.
 C(124). May 31-Aug 28.
 G(7), C(394), P(2741). May 25-Sep 16.
 C(1). Jun 16.
 G(2). Jul 18-20.
 G(3), C(3), P(1). May 31-Aug 14.
 G(9), C(100), P(1051). May 14-Sep 2.
 C(1), P(1). Jun 2-7.
 C(1), P(1). Aug 16-20.
 C(3), P(20). May 25-Jul 3; Jul 26-Aug 22.
 C(1), P(15). May 31-Jul 8; Jul 29-Aug 13.
 C(50), P(119). May 29-Sep 14.
 G(3), C(4), P(36). May 19-Jun 30; Jul 23-Sep 5.

- Semiothisa signaria* Bedford Mills, Westport. At light in sphagnum bogs, Jun 23-28, 1973.
- Semiothisa submarmorata* Westport. Common at light in sphagnum bog, Jun 27-29, 1973.
- Semiothisa transitaria* C(1). Jul 20.
- Semiothisa ulsterata* C(2), P(9). Jun 13-Jul 9; Aug 9.
- Sicya macularia* G(1), C(25), P(16). Jul 2-23.
- Spargania magnoliata* P(1). Jun 7.
- Steinoplatodes antidiscaria* C(-). One specimen at light: Jun 5, 1967.
- Stenoporpia polygrammaria* P(13). Jun 5-Jul 3.
- Sterrha demissaria* P(37). Jul 25-Aug 20.
- Synchlora aerata* G(8), C(3), P(3). Aug 11-31. Once in the spring at C: Jun 20, 1973.
- Tacparia detersata* C(5), P(33). May 18-Jul 2.
- Tacparia zalissaria* C(1), P(8). Jun 1-29.
- Tetracis cachexiata* G(24), C(47), P(98). May 16-Jul 1.
- Tetracis crocallata* G(4), C(-), P(4). Jun 2-29.
- Thera contracta* G(3), C(2), P(9). Sep 11-Oct 1; May 2.
- Thera junipereta* G(17), C(113), P(41). Oct 3-Nov 3.
- Trichodezia albiovittata* Larvae common on *Juniperus communis*. C(-), P(-). Common diurnal species in wooded locations, May 18-Sep 14.
- Triphosa haesitata* C(-), P(1). Aug 16. Three specimens at light at C: May 1-15, 1971. Adults found hibernating in cave near P.
- Venusia comptaria* C(339), P(435). Apr 29-Jun 1.
- Xanthorhoe emendata* C(7), P(17). Aug 13-Sep 9.
- Xanthorhoe ferrugata* G(20), C(30), P(72). May 14-Jun 24; Jul 15-Sep 20.
- Xanthorhoe iduata* P(1). Aug 30.
- Xanthorhoe lacustrata* C(2), P(7). May 15-Jun 2; Jul 4-Aug 5.
- Xanthotype sospeta* G(9), C(8), P(17). Jun 23-Jul 27.
- Xanthotype urticaria* G(8), C(7), P(24). Jun 17-Aug 24.
- Xystrota ferrunaria* C(16), P(21). May 10-Jul 7; Jul 20-Aug 7.
- LASIOCAMPTIDAE**
- Epincaptera americana* G(8), C(60), P(154). May 1-Jun 30; Jul 7-Aug 12.
- Malacosoma americanum* C(169), C(201), P(1190). Jun 15-Aug 1.
- Malacosoma disstria* G(2), C(86), P(132). Jun 26-Jul 31.
- Tolyte laticis* G(23), C(299), P(526). Jul 23-Sep 30.
- Tolyte velleda* G(59), C(348), P(167). Aug 15-Oct 15.
- LYMANTRIIDAE**
- Orgyia definita* C(20), P(25). Aug 15-Oct 9.
- Orgyia leucostigna* P(3). Aug 5-Oct 22. Common in Kingston in the fall of 1970, egg masses conspicuous on shade trees, especially *Acer saccharinum*.
- Parorgyia basiflava* G(1), C(3), P(32). Jul 1-Aug 18.
- Parorgyia dorsipennata* C(1), P(48). Jul 5-Aug 27.
- Parorgyia obliquata* G(9), C(40), P(460). Jul 6-Sep 1.
- Parorgyia plagiata* G(3), C(48), P(101). Jun 26-Aug 15.
- Parorgyia vagans* G(7), C(44), P(200). Jun 11-Aug 27.
- NOCTUIDAE**
- Abagrotis alternata* C(4), P(33). Jul 23-Sep 23.
- Achatodes zeeae* G(2), P(1). Jul 23-Aug 19.
- Acronicta afflicta* C(2), P(16). Jun 4-Aug 19.
- Acronicta americana* G(9), C(86), P(1215). Jun 1-Aug 26.
- Acronicta dactylina* G(14), C(27), P(168). May 30-Aug 20.
- Acronicta fragilis* C(1). Aug 9.
- Acronicta grisea* C(1). Jul 17.
- Acronicta haesitata* C(13), P(277). Jun 1-Aug 28.
- Acronicta hasta* G(7), C(27), P(105). May 21-Jul 16; Jul 13-Aug 29.
- Acronicta impleta* C(15), P(57). May 8-Jul 5.
- Acronicta impressa* G(1), P(17). May 8-Jun 29; Jul 24-Aug 26.
- Acronicta sp. near impressa* G(1). Jun 13.
- Acronicta inclara* G(2), C(24), P(106). May 31-Jul 20; Aug 10.
- Acronicta innotata* G(3), C(36), P(109). Jun 1-Aug 8.
- Acronicta interrupta* G(11), C(21), P(55). May 10-Jun 29; Jul 29-Aug 24. Frequency of melanic or partly melanic individuals in 1971 at P was 28/39 or 71.8%.
- Acronicta laetifica* G(11), C(55), P(145). May 14-Aug 10. Frequencies of melanic or partly melanic individuals: 14/32 or 43.8% (C, 1970); 20/56 or 35.7% (P, 1970); and 34/89 or 34.8% (P, 1971).
- Acronicta lanceolaria* P(1). May 31.
- Acronicta lepusculina* C(18), P(39). May 18-Jul 9; Jul 26-Aug 16.

- Acrionicta lithospila*
Acrionicta lobeliae
Acrionicta morula
Acrionicta noctivaga
Acrionicta oblinita
Acrionicta ovata
Acrionicta pruni
Acrionicta radcliffei
Acrionicta retardata
Acrionicta sperata
Acrionicta superans
Acrionicta tristis
Acrionicta tritona
Acrionicta vinnula

Adita chionanthi
Agriopodes fallax

Agroperina dubitans
Agroperina helva
Agrotis gladiaria
Agrotis venerabilis
Agrotis vetusta
Agrotis volubilis
Agrotis ypsilon

Alabama argillacea
Aletia oxygala

Amathes badinodis
Amathes bicarnea
Amathes c-nigrum

Amathes collaris

Amathes normaniana
Amathes opacifrons

Amathes smithi
Amathes tenuicula
Amolita fessa

Amphipoea americana
Amphipoea velata
Amphipyra glabella
Amphipyra pyramidoides
Amphipyra tragopoginis
Amyna octo

Anagrapha falcifera

Anaplectoides prasina
Anaplectoides pressus
Anathix puta
Anathix ralla
Anepia capsularis

Anomis erosa

Anomogyna dilvcida
Anomogyna elimata
Anomogyna youngi
Anticarsia gemmatilis
Anytus privatus
Apamea alia
Apamea amputatrix
Apamea cariosa

Apamea finitima
Apamea impulsa
Apamea inficita
Apamea inordinata
Apamea lignicolora
Apamea verbascoides

Apamea vultuosa
Apharetra purpurea
Aplectoides condita
- P(10). Jun 14-Jul 27.
 G(1), C(6), P(9). May 16-Jun 30.
 G(3), C(24), P(104). May 20-Aug 9.
 G(16), C(19), P(82). May 14-Jul 6; Jul 23.
 G(1), C(13), P(55). May 29-Jul 16; Aug 7-29.
 G(1), C(52), P(875). Jun 9-Sep 7.
 G(22), C(-), P(3). Jun 1-Jul 10; Aug 13-Sep 6.
 P(4). May 21-Jul 3.
 G(2), C(3), P(19). Jun 10-Jul 30; Aug 20.
 G(49), C(1), P(20). May 24-Jul 20.
 C(4), P(16). May 25-Jul 15; Jul 27-Aug 6.
 C(51), P(253). May 31-Aug 22; Sep 20.
 C(1), P(29). May 31-Jun 22; Jul 23-Aug 21.
 G(25), C(7), P(16). May 21-Jun 26; Jul 23-Aug 18.
 G(3), C(14), P(35). Aug 18-Oct 13.
 C(-), P(2). Jul 3-9. One specimen at light at C: Jul 12, 1967.
 G(3), C(2), P(6). Jul 3-Sep 12.
 P(8). Aug 8-19.
 G(32), C(2). Jul 30; Sep 5-23.
 G(15), C(11), P(8). Sep 5-Oct 2.
 G(1), C(1), P(1). Aug 27-Sep 13.
 G(131), C(31), P(62). May 24-Jul 5; Jul 24.
 G(226), C(48), P(112). May 8-Nov 3. Commonest in late summer and fall; apparently several overlapping generations.
 G(3). Oct 2. Migrant from the south.
 G(238), C(3), P(19). Jun 9-Jul 14; Jul 25-Oct 7.
 G(21), C(-). Sep 5-Oct 2.
 G(4), C(2), P(11). Jul 31-Sep 3.
 G(5866), C(291), P(447). Jun 1-Nov 3. Several overlapping generations; probably more than one species involved.
 C(-). Two specimens at light: Aug 28, Sep 1, 1967.
 C(5), P(42). Jul 13-Sep 27.
 P(-). One female at light in sphagnum bog: Aug 16, 1973.
 G(5), C(4), P(3). Aug 12-Sep 12.
 G(29), P(1). Aug 8-Sep 7.
 G(3), P(-). Jul 14-25. Two specimens at light in sphagnum bog at P: Jul 8, 1970.
 G(91), C(8), P(9). Jul 24-Sep 12.
 G(3), C(2), P(9). Jul 13-Aug 17.
 G(1), C(20). Jul 23-Sep 25.
 G(26), C(31), P(121). Aug 5-Oct 16.
 G(228), C(2), P(11). Jul 10-Oct 16.
 C(-). Two specimens at light: Sep 17, 1972.
 Stray from the south.
 G(68), C(3), P(11). May 29-Jul 15; Jul 23-Oct 25.
 G(2), C(3), P(19). Jun 23-Aug 29.
 C(1), P(5). Jun 18-Aug 8.
 G(1), C(1), P(1). Aug 14-Sep 2.
 C(18), P(8). Aug 14-Sep 10.
 C(-), P(1). Jul 26. One specimen at light at C: Jun 10, 1967.
 C(-). One female at light: Oct 11, 1969.
 Stray from the south.
 P(10). Aug 24-Sep 14.
 G(1), C(32), P(47). Jul 26-Sep 18.
 C(1), P(1). Jul 20; Aug 25.
 G(1), C(3). Oct 2-12. Migrant from the south.
 G(1), C(-), P(14). Sep 9-30.
 P(1). Jul 7.
 G(30), C(13), P(34). Jun 29-Aug 14.
 C(-), P(5). Jun 29-Jul 14. Once at C: Jun 17, 1967.
 G(5), C(2), P(3). Jun 10-29.
 G(6), C(2), P(1). Jun 26-Jul 25.
 C(1), P(38). Aug 8-Sep 8.
 G(6). Jun 14-26.
 G(55), C(10), P(53). Jun 16-Aug 17.
 P(2). Jul 3. One specimen at bait at P: Aug 10, 1971.
 C(1), P(3). Jun 15-24; Jul 31.
 P(1). Jul 13.
 P(3). May 31-Jun 9.

- Archanaera oblonga*
Archanaera subflava
Argyrostrotis anilis
Arzama diffusa
Arzama obliqua
Autographa ampla
Autographa biloba
Autographa mappa
Autographa precatianis

Baileya dormitans
Baileya doubledayi
Baileya ophthalmica
Balsa labecula
Balsa malana

Balsa tristigella
Bleptina caradinalis
Bombycia algens
Bomolocha abalienalis

Bomolocha baltimoralis
Bomolocha bijugalis
Bomolocha deceptalis
Bomolocha edictalis
Bomolocha madefactilis
Bomolocha manalis
Bomolocha palporia
Bomolocha sordidula
Caenurgina crassiuscula

Caenurgina erechthea

Calbe canadensis
Capis curvata
Catabena lineolata
Catocala amatrix
Catocala amica
Catocala antinymphea
Catocala blandula
Catocala briseis

Catocala cerogama
Catocala clintonii

Catocala coccinata
Catocala coelebs

Catocala concubens
Catocala crataegi
Catocala epione
Catocala gracilis
Catocala habilis
Catocala ilia
Catocala meskei

Catocala mira
Catocala neogama
Catocala obscura
Catocala paleogama
Catocala parta
Catocala piatrix
Catocala praeclara
Catocala relicta
Catocala relecta
Catocala similis
Catocala sordida
Catocala subnata
Catocala ultronina
Catocala unijuga
Ceramica picta
Cerastis tenebrifera
Cerma cora
Chaetoglaea cerata
Chaetoglaea sericea
Chamyris cerintha
Charadra deridens
Chrysanymphea formosa
Chrysaspidia contexta
Chrysaspidia putnami
Chrysaspidia venusta
- G(5), P(3). Aug 16-Sep 14.
 P(1). Jul 31.
 G(4), C(2), P(70). May 31-Jul 25.
 C(5). Aug 2-12.
 C(12), P(2). May 29-Jun 29.
 C(-), P(6). Jul 8-23.
 G(-). One specimen at light: Apr 26, 1970.
 P(1). Jul 23.
 G(32), C(15), P(17). May 24-Jul 7; Jul 26-Oct 22.
 C(23), P(123). May 19-Jul 23.
 C(3), P(21). May 31-Jun 12; Jul 13-29.
 G(1), C(29), P(220). May 4-Jun 30.
 G(30), C(7), P(185). May 20-Aug 8.
 G(30), C(9), P(16). May 31-Jun 17; Jul 22-Aug 24.
 G(1), C(5), P(14). Jun 1-Jul 9; Jul 31-Aug 13.
 G(9), C(18), P(137). Jun 11-Aug 13.
 P(1). Aug 21.
 G(3), C(10), P(54). May 21-Jul 16; Jul 25-Sep 12.
 C(18), P(331). May 19-Jul 23; Jul 27-Sep 19.
 C(2). Jul 14; Aug 22.
 G(73), P(289). May 15-Aug 25.
 C(1), P(1). Jun 2; Jul 15.
 C(9), P(11). May 29-Jul 19; Aug 9.
 C(4), P(7). May 21-Jun 26; Jul 27-Aug 20.
 C(35), P(703). May 21-Aug 25.
 C(5). Jun 15-Jul 9; Jul 31.
 G(598), C(110), P(43). May 10-Jun 26; Jul 13-Sep 19.
 G(460), C(27), P(25). May 2-Jun 24; Jul 16-Oct 20.
 C(1). Jul 19.
 C(3), P(11). Jun 20-Jul 25; Sep 4.
 G(5), C(1), P(11). May 24-Jul 8; Jul 21-Sep 6.
 G(11), C(5), P(7). Aug 28-Oct 9.
 C(-). One specimen at light: Aug 10, 1967.
 C(-), P(2). Jul 22-30. Once at C: Aug 9, 1967.
 C(1), P(7). Jul 13-Aug 24.
 C(-), P(2). Sep 15-24. One specimen at light at C: Aug 14, 1967. Four specimens collected at bait at P: Aug 12-31, 1971.
 C(16), P(46). Aug 5-Sep 23.
 G(1), C(-). Aug 5. One specimen at light at C: Jul 24, 1967. Also collected at Westbrook, Aug 11, 1963.
 G(2), C(5), P(15). Jul 20-Aug 20.
 C(-), P(7). Jul 23-Aug 17. Larvae collected on *Myrica gale* in sphagnum bog at P.
 G(8), C(6), P(21). Aug 10-Sep 28.
 G(6), C(5), P(6). Jul 14-Aug 14.
 C(4), P(142). Jul 16-Aug 25.
 C(1). Jul 20.
 G(16), C(88), P(378). Aug 15-Oct 27.
 C(15), P(70). Jul 13-Sep 23.
 C(-). One specimen at light: Sep 6, 1967; also one male at light at Amherstview: Aug 10, 1972.
 P(-). One female at bait: Aug 9, 1971.
 G(2), C(30), P(102). Aug 8-Oct 21.
 G(1), C(1), P(65). Aug 10-Oct 1.
 C(10), P(47). Jul 30-Sep 15.
 G(4), C(1), P(2). Aug 7-Oct 2.
 G(2), C(1), P(9). Aug 8-Sep 30.
 P(1). Aug 7.
 G(1), C(4), P(30). Jul 31-Oct 22.
 G(4), C(26), P(141). Aug 14-Oct 25.
 C(4), P(35). Jul 15-Aug 25.
 C(1), P(10). Jul 13-Aug 14.
 C(19), P(58). Aug 7-Oct 9.
 G(3), C(9), P(7). Jul 10-Aug 26.
 G(1), C(3), P(18). Jul 23-Oct 9.
 G(2). Jun 14; Aug 17.
 G(-), C(10), P(219). Apr 19-May 28.
 C(-), P(12). May 30-Jun 18.
 G(3). Oct 2-13.
 G(1), P(6). Sep 20-Oct 22.
 G(10), C(3), P(10). Jun 15-Jul 28.
 G(4), C(74), P(71). May 21-Aug 12.
 C(1), P(9). Jul 2-28.
 G(51), C(2), P(4). Jun 3-Jul 4; Aug 9-Oct 9.
 C(2), P(13). Jun 10-Jul 28; Aug 16-Sep 11.
 G(1), C(1). Aug 5; Sep 15.

Chytolita morbidalis
Chytonix palliatricula

Chytonix sensilis
Colocasia flavicornis
Colocasia propinquilinea
Conservula anodonta
Copivaleria grotei
Cosmia calami
Crocigrapta normani
Crymodes devastator
Cryphia villificans
Cryptocala acadensis

Cucullia asteroides
Cucullia convexipennis
Cucullia intermedia
Cucullia postera
Diarsia jucunda
Diarsia rubifera
Dipterygia scabriuscula

Dyspyralis illocata

Dyspyralis nigellus

Elaphria festivoides
Elaphria versicolor
Enargia decolor
Enargia infumata
Enargia mephisto
Eosphoropteryx thyatroides

Epiglaea apiata
Epiglaea decliva

Epizeuxis aemula
Epizeuxis americanalis

Epizeuxis concisa
Epizeuxis diminuentis
Epizeuxis forbesi
Epizeuxis julia
Epizeuxis lubricalis
Epizeuxis rotundalis
Epizeuxis scobialis
Erastris albidula
Erastris bellicula

Erastris carneola

Erastris concinnimacula
Erastris muscosula
Erastris synochitis
Erebus odora

Euagrotis forbesi
Euagrotis illapsa
Eucirrhoedia pampina
Euclidia cuspidata
Euerettagrotis perattenta
Euerettagrotis sigmoides
Euherrichia monetifera
Euparthenos nubilis
Euplexia benesimilis
Eupsilia morrisoni

Eupsilia sidus
Eupsilia tristigmata
Eupsilia vinulenta
Eurois occulta
Euthisanotia grata
Euthisanotia unio
Eutolyte electilis

Eutolyte rolandi

C(27), P(87). May 31-Jul 23.
 G(1), C(56), P(302). May 19-Aug 14. Frequency of f. *iaspis* at P was 1/101 or 1.0% (1970) and 4/201 or 2.0% (1971).
 C(2), P(28). Jul 25-Aug 22.
 G(2), C(107), P(341). May 1-Jun 18; Jul 29.
 C(6), C(45), P(37). May 4-Jun 23.
 P(6). Jul 13-26.
 G(1), C(2), P(35). Apr 12-May 29.
 G(1), C(25), P(7). Jul 14-Aug 4.
 G(13), C(80), P(812). Apr 29-Jun 13.
 G(423), C(7), P(7). Jul 3-Sep 20.
 P(17). Jun 22-Jul 28.
 C(-), P(1). Jul 29. One specimen at light at C: Aug 2, 1968.
 G(6). Jul 10-27.
 C(1), P(5). Jun 26; Jul 23-Aug 19.
 G(87), C(24), P(27). May 6-Jun 29; Jul 4-Sep 11.
 P(2). Jun 26-Jul 7.
 P(1). Jul 18.
 P(4). Aug 10-26.
 P(1). Jul 20. One specimen at bait: Aug 13, 1971.
 P(4). Jul 31-Aug 26. Collected more commonly at bait at P, especially at dusk, Aug 10-29, 1971.
 P(4). Jul 11-Aug 1. Also collected at bait at P. Lake Opinicon, one specimen resting among leaf litter: Jul 15, 1973.
 C(68), P(991). May 14-Jun 22.
 C(1), P(4). May 25-Jun 15.
 C(13), P(8). Aug 5-Sep 23.
 C(1). Jul 7.
 C(1). Jul 19.
 G(1), C(-), P(2). Aug 2-Sep 5. One specimen at light at C: Sep 17, 1972.
 P(1). Oct 2.
 G(3), C(-). Nov 2-3. One specimen at light at C: Nov 8, 1969.
 G(30), C(521), P(2087). Jun 8-Oct 14.
 G(10), C(168), P(229). Jun 9-Oct 14.
 C(1). Aug 3.
 C(3), P(60). Jul 6-Aug 12.
 C(7), P(24). Jul 11-Aug 9.
 C(1), P(56). Jul 19-Aug 29.
 G(4), C(6), P(106). Jul 10-Sep 3.
 G(1), C(162), P(1900). Jul 3-Sep 14.
 C(5), P(15). Jul 13-Aug 20.
 G(81), C(51), P(120). Jun 18-Aug 14.
 G(2), C(-), P(3). Jun 27-Jul 2. One specimen flushed in a willow field at C: Jul 10, 1969. A common diurnal species in sphagnum bogs at P, Bedford Mills, Harrowsmith, and Westport. May 25-Jul 3.
 G(62), C(66), P(107). May 24-Jul 15; Jul 16-Sep 19.
 G(1), P(1). Jun 13-19.
 G(4), C(99), P(170). Jun 13-Aug 29.
 G(43), C(55), P(35). May 31-Aug 4.
 Kingston, two specimens: Sep 23, 1958; Sep, 1961. Stray from south.
 C(5), P(89). Jun 28-Aug 10.
 G(18), C(3), P(20). Jun 9-Jul 4; Aug 8-Sep 7.
 C(1), P(18). Sep 2-Oct 16.
 G(7), C(9), P(11). May 28-Jul 17; Aug 18.
 P(2). Jul 9-15.
 P(7). Jul 6-27.
 C(9), P(89). May 30-Aug 12.
 C(-). One specimen at light: Jul 9, 1973.
 C(1), P(14). Jun 3-Jul 4; Jul 28-Aug 22.
 G(4), C(1), P(46). Oct 6-30; Apr 8-May 18. Overwinters as an adult, and like the other congeners, appears to be commoner in the spring.
 C(2), P(79). Oct 14-30; Apr 12-May 18.
 P(17). Oct 27; Apr 12-May 15.
 C(1), P(23). Oct 8; Apr 12-May 9.
 G(2), C(2), P(16). Jun 10-13; Aug 10-Sep 15.
 G(1), C(2), P(3). Jul 8-30; Sep 9.
 G(3), C(2), P(6). Jun 10; Jul 5-Aug 26.
 G(-), C(5), P(11). Apr 19-May 19. All form depilis. Typical form at Frankford: May 15, 1972.
 Wooler, four specimens at light: May 8, 1972.

- Euxoa albipennis*
Euxoa bostoniensis
Euxoa detera
Euxoa divergens
Euxoa messoria
Euxoa obeliscoides
Euxoa perpolita
Euxoa redimicula
Euxoa scandens
Euxoa scholastica
Euxoa servita
Euxoa tessellata
Euxoa velleripennis
Euxoa sp. prob ontario
Euxoa sp.
Euxoa sp.
Exyra rolandiana
- Faronta diffusa*
Feltia ducens
Feltia geniculata
Feltia herilis
Feltia subgthica
Feralia comstocki
Feralia jocosca
- Feralia major*
Fishea enthea
Galgula partita
- Graphiphora haruspica*
Haploolophus mollissima
Harrisimemna trisignata
Helicoverpa zea
Heliothis phloxiphaga
Helotropha reniformis
Hemipachnobia monochromatea
- Heptagrotis phyllophora*
Homoglaea hircina
Homohadena badistriga
Homohadena infixa
Homorthodes furfurata
Hormisa absorptalis
Hormisa bivittata
Hormisa litophora
Hormisa orciferalis
Hydroecia micacea
Hyppena humuli
- Hypenodes fractilinea*
Hypenodes palustris
- Hypocoena inquinata*
Hyppa xylinoides
- Lacinipolia anguina*
Lacinipolia implicata
Lacinipolia lorea
- Lacinipolia meditata*
Lacinipolia renigera
- Lacinipolia vicina*
Lascoria ambigialis
Lemmeria digitalis
- Leucania commoides*
Leucania inermis
Leucania insueta
Leucania phragmatidicola
- Leucania pseudargyria*
Leuconycta diphteroides
- G(1). Sep 6.
 G(1), P(6). Sep 20-Oct 2.
 G(1), C(1). Sep 4-7.
 P(1). Jul 27.
 G(2), P(3). Aug 19-Sep 15.
 G(5), C(3), P(18). Jul 28-Sep 2.
 G(1). Sep 5.
 G(6), C(1), P(32). Jul 22-Sep 4.
 G(2), P(1). Jun 29-Jul 10.
 C(4), P(10). Jul 8-Aug 15.
 C(-). One specimen at light: Jul 14, 1969.
 G(3), C(10), P(8). Jul 10-Sep 7.
 G(3), P(1). Aug 29-Sep 2.
 P(2). Aug 30-Sep 3.
 P(3). Aug 9-13.
 G(1). Jul 16.
 P(-). Amherstview, Harrowsmith, Bedford Mills, Westport and Portland. Larvae collected in Sarracenia purpurea leaves, Feb 15-Jun 30, and Jul 24-Oct 20. Overwinters in third instar.
 G(33), C(2), P(25). May 31-Jul 10; Jul 15-Sep 5.
 G(196), C(20), P(18). Jul 25-Sep 21.
 G(1), C(3), P(93). Aug 7-Sep 7.
 G(2), C(1), P(8). Jul 20-Aug 26.
 G(61), C(14), P(20). Jul 10-Sep 12.
 C(2), P(1). May 3-28.
 C(-), P(2). May 11-16. Two specimens at light at C: May 1, 1970.
 G(1), C(-), P(9). May 2-15.
 C(-), P(23). Sep 17-Oct 15.
 G(15), C(9), P(15). Jun 2-Oct 26. Commonest in late summer and fall.
 G(3), P(8). Jul 23-Aug 12.
 G(1), C(4), P(33). Jun 10-Aug 1.
 C(-), P(13). Jun 11-Aug 2.
 G(4), C(6), P(20). Sep 4-Oct 16.
 G(4), P(1). Jun 17: Jul 31-Aug 16.
 G(2), C(1), P(2). Aug 17-Sep 5.
 P(1). Jun 25. Common at light in sphagnum bogs at P, Bedford Mills, and Westport, Jun 10-Jul 7.
 C(1), P(11). Jul 6-31.
 G(-), C(1), P(17). Apr 12-May 11.
 G(3), C(8), P(44). Jul 3-Aug 9.
 C(2), P(1). Jul 6-18.
 C(7), P(15). Jul 4-Aug 7.
 G(7), C(-), P(2). Jul 5-Aug 15.
 G(7), C(1), P(1). Jul 14-Aug 14.
 C(1). Jul 29.
 G(17), C(5), P(4). Jul 6-Sep 18.
 G(1). Aug 18.
 G(15), C(3), P(12). May 4-Jul 2; Aug 2-Sep 7. Overwinters as an adult; appears commonest in the spring. Two adults found hibernating in limestone cave near Belleville, Sep 11, 1970.
 C(-), P(48). Jun 7-Jul 8; Jul 28-Sep 4.
 A small dark form, probably this species, is common in sphagnum bogs at P, Harrowsmith, Bedford Mills, and Westport, Jun 21-Jul 8, and Aug 15-Sep 9, at light and easily disturbed in the daytime.
 P(1). Aug 3.
 G(42), C(60), P(99). May 14-Jun 29; Jul 14-Sep 16.
 G(1), C(30), P(166). May 10-Jun 24.
 C(23), P(457). Aug 9-Sep 15.
 G(3), C(-). Jul 2-16. One specimen at light at C: Jun 15, 1967.
 G(42), C(8), P(27). Aug 7-Sep 5.
 G(155), C(23), P(32). Jun 16-Oct 13. Several overlapping generations.
 G(27), C(13), P(27). Jul 8-Aug 9.
 P(5). Jun 6-18; Aug 18-Sep 2.
 C(1), P(5). Sep 20-Oct 2. One specimen at light at Cranberry Lake: Oct 12, 1969.
 G(143), C(68), P(138). Jun 18-Aug 25.
 C(22), P(41). Jun 1-Aug 7.
 G(24), C(7), P(92). Jun 16-Aug 14.
 G(324), C(35), P(34). Jun 1-Jul 15: Aug 12-Oct 13.
 G(13), C(28), P(3). Jul 7-Aug 6.
 G(6), C(11), P(11). Jun 2-Jul 28.

- Leuconycta lepidula*
Lithomoia solidaginis
Lithophane amanda
Lithophane antennata

Lithophane baileyae
Lithophane bethunei
Lithophane disposita
Lithophane fagina
Lithophane grotei
Lithophane hemina

Lithophane innominata
Lithophane laticinerea
Lithophane oriunda
Lithophane patefacta
Lithophane pexata
Lithophane querquera
Lithophane semiusta
Lithophane tepida
Lithophane unimoda
Lithophane sp.
Lomonaltus eductalis
Luperina passer
Macronoctua onusta
Magusa orbiifera
Marathyssa basalis
Marathyssa inficita
Metalectra discalis

Metalectra quadrisignata
Metaleptis fishii
Metaleptis salicarium
Metaxaglaea inulta
Mocis texana
Morrisonia confusa
Morrisonia distincta
Morrisonia evicta
Nedra ramosula

Neoerastria apicosa
Neoerastria caduca
Neperigea costa

Nephelodes emmedonia
Ochropleura plecta

Ogdoconta cinereola
Oligia chlorostigma
Oligia exhausta

Oligia fractilinea
Oligia illocata
Oligia mactata

Oligia minuscula

Oligia modica
Oligia semicana
Oncocnemis saundersiana
Oncocnemis viriditincta
Orthodes crenulata
Orthodes cynica
Orthosia alurina
Orthosia hibisci
Orthosia revicta
Orthosia rubescens
Palthis angularis

Pangrapta decoralis
Panopoda carneicosta
Panopoda rufimargo
Panthea pallescens
- C(2), P(7). Jun 7-Jul 10; Aug 13.
 G(1), C(1), P(3). Sep 8-23.
 P(1). Apr 20.
 G(1), C(3), P(10). Sep 21-Oct 13; Apr 30-May 22. Adults of this species overwinter and, like other members of the genus, are more prevalent in the spring months.
 C(-), P(33). Sep 15-30; Apr 12-May 18.
 G(1), P(3). Apr 8-May 19.
 P(2). Apr 27-May 27.
 C(3), P(33). Sep 22-Oct 13; Apr 12-May 17.
 G(7), C(2), P(24). Oct 1-11; Apr 12-May 19.
 C(5), P(31). Oct 21; Apr 19-Jun 5. Frequency of f. lignicosta at P was 26/31 or 83.9%.
 P(1). May 2.
 G(5), C(1), P(16). Oct 21; Apr 8-May 21.
 G(1). Apr 8.
 P(1). May 11.
 P(14). Apr 23-May 25.
 P(1). May 11.
 C(2), P(8). Apr 27-May 23.
 P(1). Apr 23.
 G(6), C(-), P(4). Oct 10; May 3-15.
 G(1). Apr 8.
 C(2), P(2). Jun 27; Aug 2-13.
 G(6). Jun 14-Jul 14.
 G(3), P(4). Sep 7-Oct 7.
 P(137). Sep 6-Oct 14. Migrant from the south.
 G(1), C(37), P(55). May 8-Jun 18.
 G(5), C(46), P(174). May 30-Aug 29.
 C(-), P(3). Jul 29-Aug 10. One specimen at light at C: Jul 24, 1968; another at bait: Jul 15, 1969.
 G(1), C(1), P(11). Jun 10-Aug 7.
 P(4). May 11-21.
 G(-), C(1), P(13). Apr 30-May 18.
 C(1), P(2). Sep 17-21.
 P(1). Sep 13. Stray from the south.
 C(55), P(133). May 1-Jun 12.
 G(-), C(433), P(363). May 1-Jun 7.
 G(3), C(8), P(84). May 1-29.
 G(22), C(124), P(200). May 4-Jun 27; Jul 3-Sep 22.
 G(1). Jun 14.
 C(3), P(4). Jun 1-18; Jul 17-31.
 C(-), P(13). Jun 27-Aug 2. One specimen at light at C: Jun 28, 1972.
 G(83), C(65), P(91). Aug 19-Sep 30.
 G(86), C(42), P(136). May 21-Jul 15; Jul 25-Sep 18.
 G(46), C(6), P(22). Jun 10-Jul 31; Aug 3-Sep 16.
 P(1). Jul 23.
 G(2), P(1). Jul 24-Aug 9. One specimen at light at Amherstview: Aug 2, 1972.
 G(16), P(1). Jul 24-Aug 22.
 P(10). Sep 15-29.
 C(1), P(7). Sep 15-Oct 1. Larva collected on flower of Cypripedium calceolus (Jun 2, 1973 at P), and reared on C. acaule; pupated Jun 23, one male emerged Sep 12.
 H(25). Aug 15-Sep 15. Also collected in sphagnum bogs at P, Bedford Mills, and Westport, Jul 29-Sep 6, mostly at light. Form grahami rare at P, common at Westport.
 G(21), C(1), P(6). Jul 23-Sep 26.
 P(6). Jun 28-Jul 26.
 G(1), C(1). Aug 30-Sep 4.
 C(1). Sep 5.
 G(3), C(1), P(72). Jun 25-Sep 5.
 G(1), C(5), P(80). May 18-Jul 11.
 C(1). May 1.
 G(38), C(41), P(107). Apr 12-Jun 10.
 G(5), C(16), P(124). Apr 20-May 31.
 G(1), C(21), P(173). Apr 19-May 24.
 G(12), C(64), P(171). May 21-Jul 6; Jul 20-Sep 15.
 P(47). Jun 10-Aug 28.
 G(2), C(31), P(87). Jun 20-Aug 19.
 C(46), P(89). Jun 9-Aug 13.
 C(126), P(422). May 18-Jul 1; Jul 5-Aug 28.
 Apparently two generations, the second much more prevalent.

- Papaipema appassinata* P(3). Aug 26-Sep 8. Also collected at light, or as larvae in the roots of *Sarracenia purpurea*, in sphagnum bogs at P. Marlbanks, Amherstview, Bedford Mills, Westport and Portland. Larvae: Jun 30-Jul 18; adults: Aug 25-Sep 6.
- Papaipema cataphracta* G(3). Oct 2-7.
Papaipema eupatori P(2). Sep 27-30.
Papaipema furcata C(1), P(4). Sep 6-27.
Papaipema impecuniosa G(4). Oct 2-6.
Papaipema inquaesita P(5). Sep 15-Oct 9.
Papaipema lysimachiae P(1). Sep 11.
Papaipema marginidens G(1). Oct 11.
Papaipema nebris G(1). Sep 5.
Papaipema nepheleptena C(1), P(1). Sep 14-23.
Papaipema pterisii C(5), P(4). Aug 22-Sep 28.
Papaipema purpurifascia G(1), C(7), P(12). Aug 26-Oct 25.
Papaipema speciosissima P(25). Sep 9-Oct 9. Frequency of f. *regalis* was 6/25 or 24.0%.
 C(-). One specimen at light: Sep 10, 1968.
Papaipema unimoda G(7). Jun 17-Jul 3.
Paradiarsia littoralis C(1), P(33). Jun 1-Sep 7.
Parallelia bistriaris G(1), P(2). Aug 7-12.
Parastichtis discivaria G(11), C(5), P(65). Jun 23; Jul 28-Oct 27.
Peridroma saucia G(6), C(7), P(3). Jul 10-31; Sep 3-13.
Phalaenostola larentioides P(1). Jul 28.
Philometra eumelusalis C(1). Jul 17.
Philometra hanhami P(1). Aug 9.
Philometra metonalis G(13), C(16), P(30). May 25-Jul 25.
Philogophora iris C(4), P(23). Aug 15-Sep 13. Frequency of f. *y-brunneum* at P was 8/23 or 34.8%.
Philogophora periculosa G(1), C(34), P(284). Apr 29-May 22.
 G(98), C(15), P(12). Jun 5; Jul 10-Nov 3.
 Commonest in late summer and fall.
Phoberia atomaris P(21). Aug 17-Sep 4.
Platypene scabra C(4), P(56). Aug 15-Sep 15.
Platyperigea meralis P(3). Oct 1-14.
Platyperigea multifera C(1), P(19). May 25-Jun 24; Aug 1-19.
Platypolia anceps G(19), C(7), P(22). Jun 2-30; Jul 28-Sep 4.
Platysenta vecors G(3), C(2), P(10). Jun 9-Jul 15; Aug 27-Oct 2.
Platysenta videns G(1), C(1), P(3). Jun 26-Jul 28.
Plusia aerea C(-), P(1). Jul 23. One specimen at light at C: Jul 23, 1967. Also collected once at Kingston: Jul 24, 1963.
Plusia aeroides G(1). Jul 16.
Plusia balluca G(161), C(63), P(83). May 12-Jul 13; Jul 24-Sep 7.
Plusiodonta compressipalpus G(2), P(8). Jun 28-Aug 1.
Polia adjuncta G(47), P(3). Jun 2-Jul 5; Aug 8-Sep 4.
Polia assimilis C(11), P(63). Jun 15-Jul 29.
Polia atlantica G(1), C(1), P(16). May 30-Jul 10.
Polia detracta P(1). Jul 30.
Polia grandis C(9), P(77). May 15-Jul 8.
Polia imbrifera G(25), C(6), P(11). Jun 11-Aug 5.
Polia latex G(9), C(-), P(1). Jun 22-Jul 24.
Polia legitima G(1), C(2), P(46). Jun 1-Jul 15.
Polia lilacina C(2), P(5). Jul 15-28.
Polia lutra C(4), P(36). May 19-Jun 28.
Polia nimbosea G(1), C(2), P(14). Aug 7-27.
Polia obscura P(-). One male at light in sphagnum bog at P: Jun 21, 1973.
Polia purpissata C(2), P(26). Apr 12-May 19.
Polia rugosa G(37), C(2), P(16). Jun 7-Sep 14.
Polia segregata G(2), C(-). Sep 7-Oct 11. One specimen at light at C: Nov 1, 1969; another at bait: Oct 12, 1970.
Polia subjuncta G(10), P(1). Aug 2-19.
Prodenia ornithogalli C(-), P(78). Jun 9-Aug 5.
Protogrotis niveivenosa G(4), C(1). Jul 3-13; Aug 18-26.
Protocryphia secta C(1). Jul 15.
Protolampra brunneicollis G(15), C(26), P(30). May 23-Jul 12.
Protorthodes curtica G(67), C(7), P(28). May 28-Jul 1; Jul 29-Sep 4.
Protorthodes oviduca C(3), P(39). Apr 12-May 18.
Proxenus miranda P(3). Sep 17-27.
Psaphida resumens G(649), C(137), P(67). May 8-Nov 4. Several overlapping generations.
Psectraglaea carnosae G(10), C(6), P(11). Jul 7-Sep 5.
Pseudaletia unipuncta G(8), C(4), P(19). Sep 6-Oct 9.
Pseudeua purpurigera C(1), P(6). Apr 12-May 18.
Protocryphia includens C(7), P(43). Apr 12-May 29.
Pyreferra citromba G(1), P(1). Jun 20-Jul 17.
Pyreferra petiti G(7), C(224), P(1135). May 14-Aug 23.
Pyrrhia umbra
Raphia frater

- Renia factiosalis*
Renia flavipunctalis
Renia sobrialis
Rhynchagrotis anchocelioides
Rhynchagrotis brunneipennis
Rhynchagrotis cupida
Rivula propinquialis

Schinia florida

Schinia marginata
Schinia trifascia
Scoliopteryx libatrix

Scotogramma trifolii
Senta defecta
Sideridis maryx
Sideridis rosea
Simyra henrici
Spaelotis clandestina
Spargaloma perditalis
Spargaloma sexpunctata
Spodoptera exigua
Spodoptera frugiperda
Sunira bicolorago
Syngrapha alias
Syngrapha altera
Syngrapha epigaea

Syngrapha rectangula
Syngrapha selecta
Tarache terminimaculata
Tarachidia candefacta
Tarachidia erastrisoides

Trachea delicata
Tricholita signata

Trichoplusia ni
Trichoplusia oxygramma
Ufeus satyricus
Ulolonche culea
Ulolonche modesta
Xanthia flavago
Xylena cineritia
Xylena curvimacula

Xylena nupera

Xylomiges alternans
Xylomiges dolosa
Xylomoia chagnoni
Zale aeruginosa
Zale cingulifera
Zale duplicata
Zale galbanata
Zale helata
Zale horrida
Zale lunata

Zale minerea
Zale obliqua
Zale phaeocapna
Zale unilineata
Zanclognatha cruralis
Zanclognatha jachusalis
Zanclognatha laevigata
Zanclognatha lituralis
Zanclognatha ochreipennis
Zanclognatha protumnusalis
Zenobia pleonectusa

NOLIDAE
Celama cilicoides

Nola ovilla
Sarbenia minuscula
- C(10), P(255). Jul 23-Sep 4.*
G(7), C(144), P(823). Jul 10-Sep 15.
P(1). Aug 2.
P(1). Aug 14.
P(6). Jul 24-Sep 12.
C(2), P(6). Jul 30-Sep 28.
G(96), C(17), P(29). Jun 11-Jul 25; Aug 6-Sep 15.
C(2), P(1). Jul 21-29. Adults common in flowers of Oenothera, the larval foodplant.
G(1), C(2), P(3). Jul 27-Aug 14.
G(1), C(2), P(1). Jul 17-Aug 13.
G(3), C(1), P(2). Sep 1-7; May 1-16. Adults found hibernating in caves at P, Lake Opinicon, and Westport, Aug 30-Oct 25.
G(10), C(2). Jun 10-Sep 6.
P(1). Jul 24.
P(1). Jun 20.
G(21), C(3), P(86). May 23-Jul 5.
G(53), C(4), P(9). May 16-Jun 21; Jul 24-Sep 5.
G(42), C(-), P(9). Jun 20-Jul 24; Aug 6-Oct 3.
C(6), P(14). May 30-Jul 13; Aug 3.
G(1), C(34), P(96). May 30-Sep 2.
G(1). Oct 2.
G(131), C(5), P(62). Aug 17-Oct 24.
G(50), C(30), P(113). Sep 14-Nov 2.
C(1). Jul 20.
P(12). Aug 10-Sep 3.
G(1), P(-), C(1). Aug 14-Sep 5. Reared from larvae on Myrica gale in bogs at P and Portland.
C(1), P(1). Jul 3-9.
P(3). Aug 13-31.
G(2), P(2). Jun 29-Jul 10; Aug 13.
G(83), C(2), P(17). Jun 1-Jul 3; Jul 15-Aug 31.
G(88), C(4), P(24). Jun 1-Sep 16. Probably two overlapping generations.
P(1). Jul 22.
C(2), P(1). Jul 28-Aug 14. One specimen at bait at C: Jul 19, 1969.
G(24), C(-). Aug 10-Oct 11.
P(1). Sep 11.
G(1), C(3), P(5). Sep 9-Nov 4.
G(5), C(30), P(180). May 18-Jul 2.
G(1), C(6), P(60). May 14-Jun 17.
G(1), C(-), P(7). Sep 17-Oct 11.
G(5), P(2). Apr 8-May 15.
G(6), C(4), P(49). Oct 11; Apr 12-May 26.
Adult overwinterers.
G(2), C(-), P(1). Apr 30-May 4. One specimen at bait at C: Sep 21, 1969.
P(15). May 8-30.
G(-), C(16), P(26). May 1-30.
C(1), P(5). Jun 29-Jul 28.
P(8). May 30-Jul 7.
C(7), P(19). May 3-30.
C(11), P(41). May 6-Jun 6.
G(6), C(4), P(1). May 16-Jun 22; Jul 25.
G(1), C(38), P(16). May 19-Jun 29.
G(1), C(2), P(5). Jun 7-Jul 15.
G(1), C(-), P(1). Aug 4; Oct 11. One specimen at light at C: Nov 2, 1969; another at bait: Oct 24, 1970.
G(1), C(168), P(152). May 1-Jun 30.
C(2). May 8-Jun 1.
C(31), P(42). May 1-Jun 7.
C(4), P(3). May 11-Jun 11.
C(11), P(10). Jun 13-Jul 9.
C(4), P(4). Jul 12-Sep 9.
C(16), P(110). Jul 11-Aug 25.
C(2), P(21). Jun 23-Aug 2.
G(5), C(125), P(887). Jul 10-Sep 14.
G(4), C(18), P(22). Jul 2-Sep 2.
G(1), C(5), P(3). Jul 16-Sep 11.

G(1), C(-). Aug 5. Two specimens at light at C: Jul 6-10, 1970 (ROM).
C(3). May 12-25.
G(3), C(9), P(67). Jun 12-Aug 3. Possibly more than one species involved.

NOTODONTIDAE

- Cerura borealis* C(3), P(33). May 31-Jun 16; Jul 1-Aug 13.
Cerura cinerea G(3), C(49), P(128). May 25-Jul 25; Jul 23-Aug 25.
Cerura modesta G(5), C(13), P(43). May 6-Jun 7; Jul 15-Aug 15.
Cerura multiscripta C(2), P(2). May 30-Jun 19. All females, males apparently diurnal. Reared from larvae collected on *Populus grandidentata*.
Cerura occidentalis G(5), C(17), P(30). May 8-Jul 1; Jul 11-Aug 20.
Clostera albosigma G(3), C(191), P(264). May 3-Jun 25; Jun 22-Aug 23.
Clostera apicalis G(3), C(20), P(19). May 16-Jun 19; Jul 27-Aug 20.
Clostera strigosa C(2), P(4). May 30-Jun 22.
Dasylophia thyatiroides C(4), P(5). May 23-Jun 18; Aug 5-16.
Datana angusi C(23), P(39). Jun 14-Aug 1.
Datana contracta G(9), C(5), P(38). Jun 7-Jul 31.
Datana integerrima C(1). Jul 18. More common in previous years at C: Jun 13-Aug 10.
Datana ministra G(7), C(26), P(101). Jun 2-Aug 2.
Datana perspicua G(11), C(1), P(13). Jul 7-Aug 13.
Ellida caniplaga G(7), C(218), P(120). May 1-Jul 25; Oct 2.
Gluphisia avimacula C(35), P(106). May 2-Jun 11.
Gluphisia leptneri G(3), C(-), P(7). Apr 23-May 11.
Gluphisia septentrionis G(21), C(209), P(535). May 8-Jul 6; Jul 3-Aug 26.
Heterocampa bilineata G(21), C(12), P(23). Jun 2-Jul 10; Jul 23-Aug 26; Sep 27.
Heterocampa biundata C(20), P(28). Jun 8-Jul 31.
Heterocampa guttivitta G(2), C(522), P(484). May 5-Jul 21; Aug 20; Sep 10.
Heterocampa manteo C(-). One specimen at light: Jul 23, 1968.
Heterocampa obliqua C(17), P(65). Jun 2-Aug 8.
Heterocampa umbrata C(49), P(89). May 31-Jul 28.
Hyperaeschra georgica G(1), C(18), P(51). May 14-Jul 14; Aug 10.
Macrurocampa marthesia G(8), C(106), P(386). Jun 19-Aug 25.
Nadata gibbosa G(2), C(215), P(586). May 21-Aug 22.
Nerice bidentata G(26), C(62), P(104). May 14-Aug 22.
Notodonta simplaria G(2), C(5), P(5). May 16-Jun 13; Jul 16-Aug 12.
Notodonta stragula C(9), C(20), P(60). May 31-Jul 10; Jul 18-Aug 17.
Odontotia elegans G(2), C(38), P(46). May 21-Jul 11; Jul 15-Aug 25.
Oligocentria lignicolor C(24), P(244). Jun 13-Aug 16; Sep 3.
Peridea angulosa G(12), C(169), P(543). May 31-Jul 5; Jul 3-Aug 31.
Peridea basitriens C(8), P(38). Jun 13-18; Jul 10-Aug 2.
Peridea ferruginosa G(2), C(165), P(202). May 29-Jun 28; Jun 29-Aug 24.
Phaeosia rimosa G(4), C(113), P(195). May 8-Jul 18; Jul 16-Sep 15.
Schizura apicalis C(-), P(9). Jun 1-10; Jul 13-26.
Schizura badia C(5), P(38). Jun 11-Aug 9.
Schizura concinna G(1), C(2), P(5). Jul 23-Aug 12.
Schizura ipomeae G(4), C(29), P(51). Jun 19-Aug 7.
Schizura leptinoides G(4), C(512), P(1610). May 21-Sep 14. Probably two or more overlapping generations.
Schizura semirufescens G(5), C(41), P(117). Jun 12-Aug 16.
Schizura unicornis G(33), C(83), P(138). May 19-Aug 22.
Symmerista albifrons C(4). Jun 21-22.
Symmerista canicosta C(26), P(66). Jun 8-Jul 23.
Symmerista leucitys C(30), P(39). Jun 7-Jul 17.

SATURNIIDAE

- Actias luna* G(1), C(142), P(750). May 14-Jul 30.
Antheraea polyphemus G(11), C(19), P(89). Jun 2-Jul 28.
Automeris io G(6), C(101), P(168). May 30-Jul 4.
Callosamia promethea C(-), P(-). Several females at light in 1972 at C. Diurnal males attracted to caged, laboratory-bred females at C and P, Jun 10-Jul 8. Larvae reared on *Prunus*. Previously common in the city of Kingston, feeding on *Syringa*.
Hyalophora cecropia G(2), C(19), P(36). May 29-Jun 20.

SPHINGIDAE

- Amphion nessus* G(-), C(-), P(-). Diurnal, May 24-Jul 10, visiting flower blossoms (especially *Syringa*) and carrion. Larvae collected on *Vitis riparia*.

- Ceratonia amyntor*
Ceratonia undulosa
Cressonia juglandis
Darapsa myron
Darapsa pholus
Darapsa versicolor
Deidamia inscriptum
Dolba hylaeus
Eumorphia achemon
Eumorphia pandorus
Hemaris diffinis
Hemaris thysbe
Hyles lineata
Lapara bombycoides
Manduca quinquemaculata
Pachysphinx modesta
Paonias excaecatus
Paonias myops
Smerinthus cerisyi
Smerinthus jamaicensis
Sphecodina abbottii
Sphinx canadensis
Sphinx chersis
Sphinx drupiferarum
Sphinx eremitus
Sphinx gordius
Sphinx kalmiae
 THYATIRIDAE
Euthyatira pudens
Habrosyne scripta
Pseudothyatira cymatophoroides
Pseudothyatira expultrix
 ZANOLIDAE
Apatelodes angelica
- G(11), C(27), P(67). May 31-Aug 16.
 G(6), C(176), P(1026). May 8-Sep 7. Bimodal flight period, with peaks in mid-June and mid-to late July.
 G(1), C(41), P(144). May 14-Jun 19; Jun 29-Aug 1; Aug 26.
 G(19), C(39), P(34). May 31-Aug 10. Larvae common on *Vitis riparia*.
 G(2), C(19), P(92). May 21-Aug 12.
 C(1), P(14). Jun 28-Jul 29.
 G(2), C(4), P(6). May 6-30.
 P(5). Jun 17-Jul 14.
 G(7), P(1). Jul 3-Aug 14.
 C(1), P(7). Jul 10-Aug 14. One larva collected on *Vitis riparia* at Lake Opinicon; formerly common on *Parthenocissus* in Kingston.
 C(-), P(-). Common diurnal species, May 12-Jul 31, frequently visiting *Syringa* blossoms; observed ovipositing on *Lonicera*.
 C(-), P(-). Diurnal, May 29-Jun 9, visiting mostly *Syringa* blossoms.
 C(1). Aug 15.
 G(3), C(265), P(604). May 31-Aug 10.
 G(12), C(-). Jul 16-Aug 12.
 C(27), P(48). May 31-Aug 15.
 G(13), C(108), P(238). May 29-Aug 18.
 G(31), C(60), P(140). May 24-Aug 17.
 C(58), P(38). May 4-Jun 26; Jul 11; Jul 30.
 G(10), C(23), P(75). May 23-Aug 22. All f. norm. *geminatus* except for two typical *jamaicensis* from P.
 C(4), P(13). May 6-Jun 19. Larvae collected on *Vitis riparia*.
 G(2), C(1), P(5). Jun 12-Jul 29.
 G(14), C(7), P(102). Jun 10-Aug 22.
 G(37), C(4), P(3). May 31-Aug 5.
 C(-). One male at light: Jul 8, 1974.
 G(5), C(26), P(126). May 19-Jul 28; Aug 15.
 G(6), C(9), P(32). Jun 1-Aug 13.
 C(2), P(26). May 1-30. Includes two individuals of form *pennsylvanica* from P.
 G(1), C(1), P(2). Jul 13-28.
 C(2), P(2). Jul 14-Aug 1.
 C(2), P(1). Jun 22-Jul 28. Other records: P, Aug 10, 1971 (at bait), Jun 21, 1973 (at light in bog); Westport, Jun 29, 1973 (at light in bog).
 C(26), P(272). Jun 8-Aug 11.

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A NEW SPECIES OF HYPAGYRTIS (GEOMETRIDAE)

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ABSTRACT

A new species, *Hypagyrtis brendae*, is described from Arkansas, Kentucky and Missouri. This new species varies from all other known *Hypagyrtis* species in three characteristics: the coloration, the angular relation of the postmedial and medial lines to the inner margin and the postmedial line formation. The male and female types and the male genitalia are figured. The male and female types have been deposited in the United States National Museum.

INTRODUCTION

AFTER SEVERAL YEARS of extensive investigation of the *Hypagyrtis*, it was revealed that there was an undescribed species occurring in scattered colonies throughout the Midwestern United States. This is supported by three outstanding characteristics: the coloration, the angular relation of the postmedial and medial lines to the inner margin and the postmedial line formation. The genitalia of this new species shows no satisfactory differences from the other members of the genus. The new species exists sympatrically with *H. subatomaria* (Wood) 1839. It is a multi-voltine species with two broods, the second brood being the least common. Its habitat is an acid soil, forest environment in Missouri and Arkansas. It has only been captured in Northwestern Arkansas, North Central Kentucky and Eastern Missouri.

***Hypagyrtis brendae* R. L. Heitzman, new species**

MALE: Head: Vertex and front heavily scaled with gray; eyes black; palpi short and gray, extending beyond front about one third diameter of eyes; antennal stalk gray with sprinkling of black scales, pectinations brown.

Thorax: Above, gray, patagia gray extending beyond base of hindwings; below, gray with fine hairs, legs, gray with scattered black scales.

Abdomen: Above, gray with scattered black scales; below, uniformly gray.

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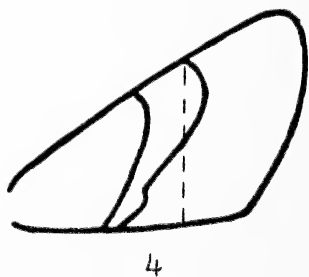
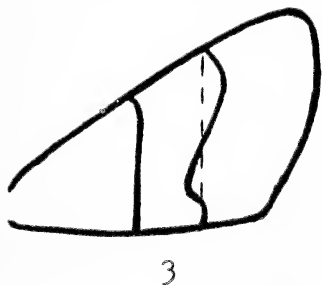


Fig. 1.—*Hypagyrtis brendae*, new species, holotype male, Washington State Park, Washington Co., Missouri, 5 June 1973 (J. R. Heitzman) X 1.75

Fig. 2.—*Hypagyrtis brendae*, new species, allotype female, Washington State Park, Washington Co., Missouri, 7 June 1973 (R. L. Heitzman) X 1.75

Fig. 3.—Diagrammatic drawing of right forewing of typical *Hypagyrtis* spp.

Fig. 4.—Diagrammatic drawing of right forewing of *Hypagyrtis brendae*.

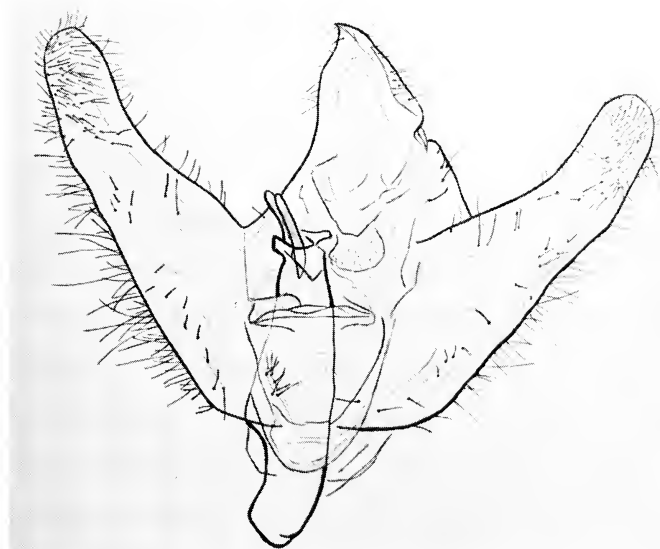
Wings: Dorsal surface: Forewings, ground color gray with scattered black scales except where invaded by small and restricted areas of brown, brown in varying amounts occurs between the subterminal and postmedial lines, along costal margin and basal area; fringe, alternating patches of dark and light scales on outer margin, long hairs on inner margin; subterminal line, white, rarely complete and with white subterminal spot in cell R_5 ; postmedial line, black, complete, convex to subterminal spot and extending nearly straight beyond to inner margin where it enters at a basally inclined angle; medial line, black, diffuse, usually incomplete and entering inner margin obliquely; distal spot, black; antemedial line, black, usually complete. Hindwings, concolorous with forewings but paler at costal and basal areas with brown present only between postmedial and subterminal lines; fringe, as forewings; subterminal line white, rarely complete; postmedial line, black, fading at costal margin; distal spot, black; medial line, black, broad and diffuse, fading at costal margin; gray hairs present in basal area. Ventral surface: Forewings, pale gray scattered with black scales; postmedial line, black, always present; distal spot, black; weak diffuse line sometimes present inside distal spot, outwardly inclined in contrast to postmedial line. Hindwings, concolorous with forewings; postmedial line, black, complete, no fading at costal margin; distal spot, black; medial line, black, sometimes incomplete, again no fading at costal margin.

FEMALE: Same as male; except larger, often lighter and outer margins more scalloped.

ETYMOLOGY: I take pleasure in naming this species for my sister Brenda Heitzman.

FOREWING LENGTH OF TYPE SERIES: Spring brood: Average for 275 males 16.40 mm, range 14-17 mm; for 30 females 19.86 mm, range 18-21 mm. Summer broods: Average for 25 males 12.75 mm, range 12-14 mm; for 3 females 16.50 mm, range 15-17 mm.

TYPES: Holotype, male, Washington State Park, Washington Co., Missouri, 5 June 1973 (J. R. Heitzman); allotype, female, Washington State Park, Washington Co., Missouri, 7 June 1973 (R. L. Heitzman); 299 male and 32 female paratypes: from the type locality: five males and two females, 6 June 1972 (J. R. Heitzman); 70 males and five females, 5 June 1973 (J. R. Heitzman).



5

Fig. 5.—Male genitalia, *Hypagyrtis brendae*, new species, holotype, ventral view. X 31

man); 40 males and seven females, 5 June 1973 (R. S. Funk); 13 males, 7 June 1973 (J. R. Heitzman); 123 males and two females, 7 June 1973 (R. L. Heitzman); nine males and one female, 18 August 1973 (R. L. Heitzman); five males, 18 August 1973 (J. R. Heitzman); five males, 22 August 1973 (J. R. Heitzman); five males and one female, 22 August 1973 (R. S. Funk); from Dr. E. A. Babler State Park, St. Louis Co., Missouri: seven males, 6 June 1973 (J. R. Heitzman); from Blue Springs State Park, Washington Co., Arkansas: one male and one female, 29 May 1966 (R. L. Heitzman); two females, 29 May 1966 (J. R. Heitzman); one female, 27 May 1967 (R. L. Heitzman); one female, 27 May 1967 (J. R. Heitzman); two females, 31 May 1971 (R. L. Heitzman); one male and two females, 4 June 1971 (J. R. Heitzman); one female, 4 June 1971 (R. L. Heitzman); two females, 6 June 1971 (J. R. Heitzman); one male and one female, 21 August 1971 (J. R. Heitzman); three males and one female, 27 May 1972 (R. L. Heitzman); seven males, 27 May 1972 (J. R. Heitzman); from Leslie Farm, Nelson Co., Kentucky: two males, 23 June 1971 (G. Florence); from Bardstown, Nelson Co., Kentucky: one male, 29 April 1970 (G. Florence); from Horner Bird Sanctuary, Oldham Co., Kentucky: one male, 22 June 1966 (C. V. Covell, Jr.).

TYPE LOCALITY: Washington State Park, Washington Co., Missouri, in forested area.

LOCATION OF TYPES: The holotype and allotype will be deposited in the type collection of the United States National Museum, Washington, D.C. Paratypes will go to the following institutions and individuals: The Florida State Collection of Arthropods, Gainesville, Florida; American Museum of Natural History, New York, New York; The Entomology Museum of the University of Missouri, Columbia, Missouri; Central Missouri State University, Warrensburg, Missouri; Dr. A. E. Brower, Augusta, Maine; Dr. C. V. Covell, Jr., University of Louisville, Louisville, Kentucky; Richard S. Funk, Illinois State University, Normal, Illinois; Dr. W. C. McGuffin, Biosystematics Research Institute, Ottawa, Ontario; Laurence R. Rupert, Sardinia, New York; and the Heitzman collections.

DISCUSSION

The coloration of *H. brendae* is unique among the *Hypagyrtis*, as no other species possesses such a color scheme and pattern. The angular relation of the postmedial and medial lines of the forewing to the inner margin of *H. brendae* is strongly oblique (fig. 4); whereas, with all the other *Hypagyrtis* these lines are almost perpendicular to the inner margin (fig. 3). The forewing postmedial line formation of *H. brendae* is nearly straight beyond the st. spot (fig. 4), while in the other species it is deeply concave and jutting to the inner margin (fig. 3). Finally, the subterminal line of *H. brendae* occurs rarely among the rest of the genus.

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I am grateful for the assistance of Dr. A. E. Brower, Augusta, Maine; Dr. C. V. Covell, Jr., University of Louisville, Louisville, Kentucky; Dr. Douglas C. Ferguson, United States National Museum, and Dr. Frederick H. Rindge, American Museum of Natural History for determinations and comments on the *Hypagyrtis*. Also, I wish to thank Richard S. Funk, Illinois State University, Normal, Illinois, for his field assistance.

LITERATURE CITED

WOOD, 1839. *Index Entomologicus*, p. 241, fig. 1673.

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GENETIC CONTROL OF MACULATION AND HINDWING COLOR IN *APANTESIS PHALERATA* (ARCTIIDAE)¹

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THE TIGER MOTH *Apantesis phalerata* (Harris) is a common representative of the family Arctiidae around Gainesville, Florida. During the course of a recent investigation (Bacheler, 1972) of its biological and systematic relationship with a sibling species, *A. radians* Walker, rearing studies revealed information on the inheritance of certain pattern elements in the adult stage. The normal adult male of this species has yellow hindwings and lateral abdominal stripes, and a criss-cross pattern of cream bands across black forewings. The normal female has red hindwings and abdominal stripes, and only one cream band (with a parallel, short cream bar) on black forewings (Fig. 1). This paper reports data on the genetic control of the forewing and body maculation and on the sex-limited expression of the gene controlling hindwing coloration in *Apantesis phalerata*.

METHODS

As part of life history studies on *A. phalerata*, field-collected females were brought into the laboratory for oviposition. Resulting larval broods were reared through to adulthood on an artificial diet, modified slightly (Table I) from that used by Shorey and Hale (1965).

Among the typical offspring of a phenotypically normal female (red hindwings, full maculation) collected in March 1969 were three unusually light males (almost devoid of maculation) and several females with yellow hindwings. The exact pheno-

¹Fla. Agricultural Experiment Station Journal Series No. 4559.

typic ratio in these F_1 adults was not noted since these moths were among the first reared in connection with other studies. However, each of the light males was mated to separate sibling females having the yellow hindwings. The larvae resulting from the one successful mating were reared through to adulthood. After several additional unsuccessful F_2 crosses, the F_2 progeny were then spread, labeled, and stored for later analysis.

RESULTS

Thirty-nine males and 35 females resulted from the successful mating of one of the light F_1 males to a yellow-hindwinged female sibling. Female F_2 adults were of two patterns. The first pattern was that of a typical *phalerata* female, except the normally red secondaries and abdominal area were light yellow. All 29 females displaying this pattern were uniform in expression. In the second pattern the red areas were again replaced by yellow, but there was also a loss of black maculation, resulting in females that were nearly all yellow. The typical black marginal and submarginal spots of the secondaries were absent and the black costal margin faded slightly proximally. One female of the six showing this loss of maculation had traces of submarginal spots. Only traces of postcostal maculation remained on the primaries. The patagium was entirely yellow, one female having a trace of the typical black spot. The tegulae were likewise yellow, devoid of the usual black bands. The antennae and underside of the abdomen had a few yellow scales. Both are normally black. The black dorsal abdominal stripe was considerably reduced. The two F_2 female patterns are shown in Fig. 1a-b.

About half of the 39 males showed a pattern gradation from almost typical *phalerata* males to those almost completely devoid of maculation. The other half were normal. In the transition through the series, the yellow costal stripe and postmedian transverse, subterminal W-shaped, and submedian longitudinal bands widened and fused. The black spots of the patagium, tegulae, and dorsal abdominal stripe also were reduced through the series. Four males in this transition are shown in Fig. 1d-g.

A discontinuity was noted among males which exhibited a gradation between absent maculation and normal marking. The lighter forms of one class retained most of the dark, posterior

forewing band, some of the marginal spot enclosed by the W band and the wing margin, and a distinct dorsal abdominal stripe as in normal males. The second class of nine males, containing all light forms, lacked the forewing band and marginal spot, and the dorsal abdominal stripe was reduced. The abdominal stripe, then, easily separated all the males into two distinct classes: normal (with variable expression of wing maculation in some of those males) and light. The ventral wing surfaces also easily separated the two classes. The light class lacks the one black spot near the forewing margin, and the proximal black bar along the leading edge of the forewing is broken, not solid as in the normal class (see Fig. 2). The light F_1 male successfully mated in the laboratory belonged to the first class, with a distinct dorsal abdominal stripe and solid forewing bar.

Kimball (1965) reported an aberrant male almost devoid of maculation from Gainesville, Florida, in 1959. This specimen appears identical to several in the F_2 experimental series of males. Another light male was found in July 1968 in Gainesville. It also fits well into the series, but at a slightly different point. These two wild specimens are shown in Fig. 1h-i. A third light male was found in Bradenton, Florida, in 1970. These aberrations were the only noticeably light *phalerata* found among more than 2,000 males collected during this study.

When this rare aberration of *phalerata* is collected in the future, it is hoped that an awareness of the simple mutant character of this strain will avoid taxonomic confusion and the unnecessary naming of "forms" or "species."

GENETIC ANALYSIS

The rearing of this aberrant series shows that this light form is probably inherited in simple Mendelian fashion, though the 74 progeny of the successful cross showed a considerable range of variation in maculation expressed by the controlling genotypes. One autosomal gene appears to control maculation. A simple dominant allele at this locus causes maculation and its recessive allele in the homozygous state accounts for the rare, light forms. In males, expression of the heterozygous genotype is variable.

The genotype of the original field-collected (dark, red hindwings) parental female was, according to this genetic hypothesis, heterozygous: $DdRr$. If it were homozygous for dark maculation, no light offspring would have resulted, and if it were homozygous recessive, its own phenotype would have been light. Likewise, if it were homozygous for red hindwings, none of the offspring would have had yellow hindwings, and if it were homozygous recessive it would have had yellow hindwings.

The light aberrant male reported by Kimball and examined by us was probably a recessive homozygote for maculation while the light males found in Gainesville and Bradenton were heterozygotes.

This genetic explanation on the inheritance of hindwing coloration and maculation does have the drawback of necessitating the capture of an apparently very rare female in nature, and further, having this female mate with a rare male. However, our two-gene explanation was the simplest and the only one which fit the classes of moths so precisely. A test cross would have made the hypothesis more convincing, but was not possible at the time. Since we are not planning future work on this problem, these partial results are published in the hope of stimulating further genetic investigations on these interesting arctiids.

Hindwing color seems to be controlled by a second gene locus. The dominant allele, responsible for red hindwings, is expressed only in the female. Male hindwings are yellow, regardless of the presence of this dominant gene. The homozygous recessive state of this gene in the female results in yellow hindwings.

In the following hypothetical analysis, D represents the dominant gene for expression of maculation and d its recessive allele. R designates the gene for red hindwings and r its recessive allele for yellow.

The male and female successfully crossed in the laboratory can each have only one genotype if one follows this hypothesis. The parental genotypes, their observed and expected offspring, and X^2 values are shown below. The observed and expected numbers for both male and female moths of the laboratory cross do not differ significantly from a 3:1 ratio.

Parents: F₁ ♂ X F₁ ♀
 Ddrr (Dark partly expressed) Ddrr (Dark; yellow hindwings)

Offspring: F₂ ♀♀

Genotype	Class	Expected ratio	No. Observed	No. Expected
DDrr or Ddrr	Dark	3	29	26.25
ddrr	Light	1	6	8.75

Totals 35 35

$$\chi^2 = 0.770$$

F₂ ♂♂

Genotype	Class	Expected ratio	No. Observed	No. Expected
DDrr or Ddrr	Dark	3	30	29.25
ddrr	Light	1	9	9.75

Totals 39 39

$$\chi^2 = 0.009$$

ACKNOWLEDGMENTS

We thank Dr. Dale H. Habeck, Department of Entomology and Nematology, University of Florida, who provided facilities, advice, and commented on the manuscript. This research was supported in part by NSF Grants GB8442 and GB32151 (to Thomas C. Emmel) and USDA Cooperative Agreement 12-14-100-9397 (33) (D. H. Habeck, Principal Investigator).



Fig. 1.—Various forms of *Apantesis phalerata*. (a) light, homozygous female; (b) dark female (normal female); with full maculation; (c) light male; with full maculation; (d) dark male with full maculation; (e) heterozygous male showing partial expression of maculation; (f,g) light, homozygous males; (h) wild male collected in Gainesville, Florida, heterozygous for maculation; (i) light, homozygous male reported by Kimball (1965).

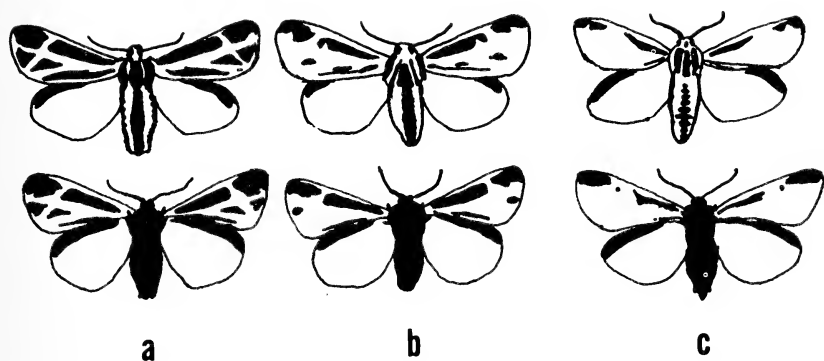


Fig. 2.—Dorsal and ventral surfaces of (a) normal homozygous males; (b) heterozygous males, and (c) light homozygous males of *Apantesis phalerata*. See text for discussion of maculation differences between the classes.

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Table 1. Modified Shorey and Hale (1965) artificial diet for rearing *Apantesis phalerata*.

Pinto beans (soaked overnight)	640 gm
Brewer's yeast*	100 gm
Ascorbic acid*	10 gm
Sorbic acid*	3 gm
Methyl p-hydroxybenzoate**	6 gm
Formaldehyde (37%)	6 ml
Agar*	40 gm
Water; with agar	800 ml
with dry ingredients	1000 ml

*Nutritional Biochemicals Corp., Cleveland, Oh.

**Fischer Scientific Co., Atlanta, Ga.

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NATURAL AND LABORATORY OCCURRENCE OF "ELYMI" PHENOTYPES IN *CYNTHIA CARDUI* (NYMPHALIDAE)

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THE "ELYMI" SERIES OF ABERRANT PHENOTYPES, characterized by suppression of the discal wing pattern, fusion of the dark subapical pattern elements, and development of a series of white submarginal spots, occurs in at least three species of the Holarctic genus *Cynthia*: *C. annabella* Field (= *C. carye* auct.), *C. virginensis* Drury, and *C. cardui* Linnaeus. The seasonal distribution and frequency of these phenotypes in wild populations of *C. annabella* in central California were recently reviewed by Shapiro (1973).

Cynthia cardui in California is a migratory species which rarely, if ever overwinters north of the Transverse Ranges. Transient populations occur in most of the state most years, generally shifting northward and upslope in mid-summer and sometimes showing a definite return flight southward in autumn. Although specimens representing various stages in the "elymi" series have been taken in many localities in California, no systematic search for them has been linked to seasonal movements and abundance of the species. The exceptionally large 1973 flight of *C. cardui* proved an opportunity for such an investigation.

In 1972, an "average" year, *C. cardui* was present in the Sacramento Valley from the third week of March to the first week in October, with the largest numbers flying in April, May, and the first half of June. No "elymi" phenotypes were reported anywhere in central California in 1972. In 1973 *C. cardui* first appeared the fourth week of February and reached "outbreak" proportions by mid-April. Very large populations persisted in the Valley until the third week of June, when most of the insects emigrated northward and upslope into the Sierra Nevada. During this period three generations appeared, feeding primarily on

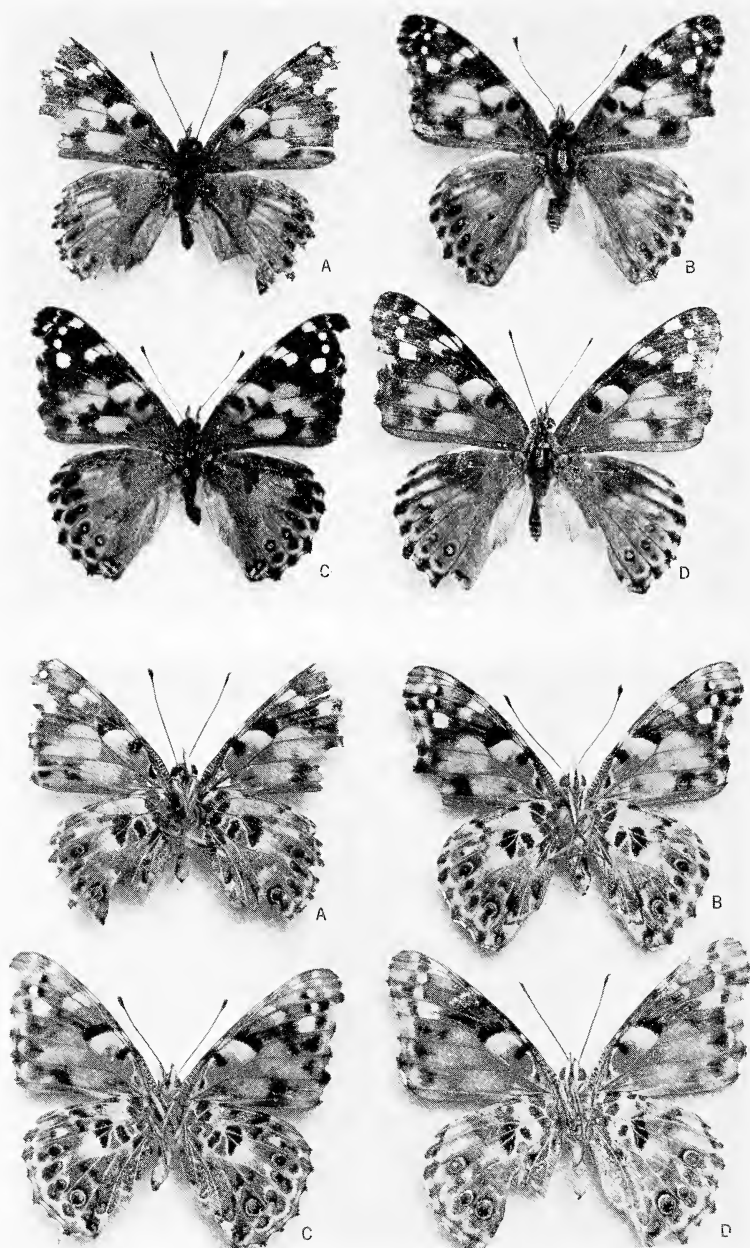


Fig. 1. — Aberrant *Cynthia cardui* collected in central California in 1973, upper and lower surfaces. For localities see text. A, v.25; B, vi.8; C, vi.2; D, ix.7.

Silybum marianum (L.) Gaertn. (Compositae), *Amsinckia* spp. (Boraginaceae), and *Malva*, spp. (Malvaceae). *C. cardui* remained in the Valley at low density through the hottest part of summer and occasional larvae could be found on *Centaurea solstitialis* L. (Compositae). From late August through September a significant southward movement through the Valley was observed. In the Sierra Nevada *C. cardui* was abundant in July and August and a major southward migration occurred in September at the same time as that in the Valley. Larvae were taken from *Cirsium* spp. and *Wyethia mollis* Grey (both Compositae). During the 1973 season five "elymi" phenotypes were reported in the Valley and two in the Sierra Nevada. An estimated 30,000 *C. cardui* were examined in the field during the season, giving a frequency of .00023, much below the .001 frequency observed for the corresponding phenotype of *C. annabella* (Shapiro, 1973).

Records of "elymi" specimens follow:

Sacramento Valley: American River, Sacramento (City) Co., California, v. 25:73 (♂), vi. 2.73 (♂ and second seen, sex undetermined); vi. 8.73 (♂). Broderick, Yolo Co., California, vi. 24.73 (seen, sex undetermined). (All A. M. Shapiro)
Sierra Nevada: East of Jerseydale, Mariposa Co., California, vi. 21.73 (♂) (O. Shields); Donner Pass, el. 7000': Placer Co., California, ix. 7.73 (♂) (A. M. Shapiro)

All of the captures except the Jerseydale specimen are shown in figure 1.

The most interesting aspect of this series is the cluster of records from the American River. All four specimens (the one missed on vi. 2 is definitely not the same individual taken vi. 8) were taken within an area one-half mile square and were in similar condition. Since *C. cardui* had been flying at the American River since March 2 they were probably locally bred, rather than immigrant individuals. Moreover, no aberrant specimens were seen at other Valley localities with equally dense *cardui* populations, despite comparable search. It is therefore likely that these four were siblings or at least that the "elymi" phenotype had a common (genetic or environmental) origin in all of them.

Dimock (1968) reported the induction of "elymi" phenotypes by holding fresh pupae of *C. cardui* at 36°F for 14 days. During the 1973 season numbers of large larvae of *C. cardui* were collected in the Valley and Sierra and the resulting pupae subjected to this treatment. Considerable variation occurred among the 37 adults obtained, but only seven were wild-type. In the remaining

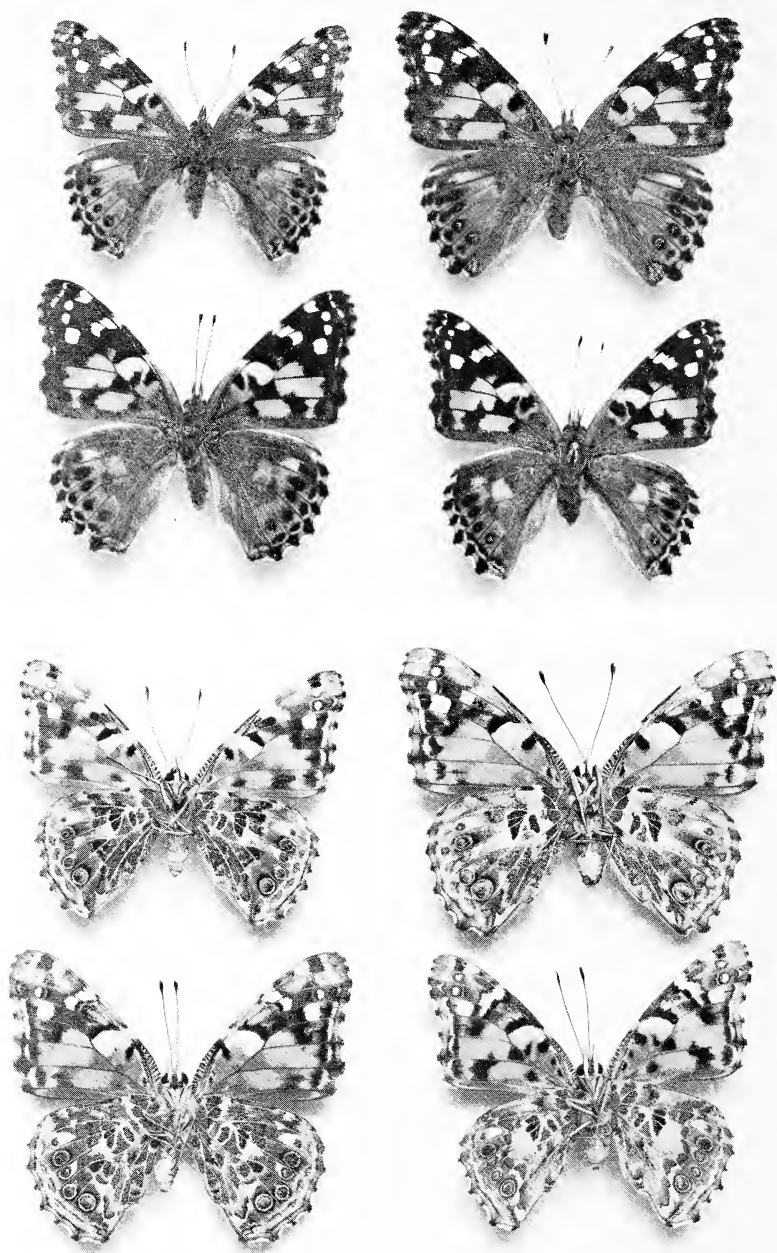


Fig. 2. — Aberrant *C. cardui* produced by chilling pupae at 36°F for 14 days. Upper and lower surfaces.



Fig. 3. — Normal *C. cardui* from pupae held at 90°F for 14 days. Upper and lower surfaces.

30 the pattern was more or less modified in the direction of "elymi" (occasionally on only the fore- or hindwings) (figure 2). Four specimens were indistinguishable from the wild "elymi" phenotypes. An additional 28 pupae died. Many of these developed fully but failed to eclose; all which had developed a pattern were "elymi," and a few were as extreme as Dimock's figure. In the control group of 30 unchilled pupae, 24 adults were obtained, all wild-type.

The dates and localities of the 1973 "elymi" (except the ix. 7 specimen) virtually exclude sustained (or severe but intermittent) chilling of the pupa as a causative agent. In an effort to determine if heating, a more likely factor afield, could induce "elymi" 21 pupae were subjected to 90°F until they hatched or for 14 days, whichever happened first. Three pupae so treated produced wild-type adults (Fig. 3) within 7 days; the remainder all died without depositing adult pigment.

"Elymi" phenotypes are produced with considerable regularity when fresh pupae of *C. cardui* are chilled, whether they come from low or high elevations. The individual batches tested are too small for any statements to be made as to the variance within local populations or among sibs with respect to this character, but it appears that the potential to produce "elymi" under temperature shock is inherent in normal *cardui*. The most promising hypothesis is that wild specimens of "elymi" are produced by genes or gene combinations which alter the threshold for expression of "elymi" so that it is produced under ordinary developmental conditions. This would make the experimental animals phenocopies, a familiar situation in genetics and one which predisposes to the evolution of phenotypic switch mechanisms through the mechanism called "genetic assimilation" (cf. Waddington, 1957). The occurrence of the phenotype in three species of *Cynthia* suggests that it may indeed have been a seasonal phenotype at one time in the evolution of the genus and that its expression was subsequently suppressed in a manner akin to the summer phenotype of *Pieris virginiensis* (Shapiro, 1971).

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DAS NATURHISTORISCHE MUSEUM IN WIEN UND SEINE LEPIDOPTERENSAMMLUNG

Von Dr. FRITZ KASY

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DAS WIENER NATURHISTORISCHE MUSEUM gehört zu den ältesten naturgeschichtlichen Sammlungen der Welt und zu den grössten dieser Art. Seine Anfänge reichen bis in das Jahr 1748 zurück, in dem vom damaligen Herrscher von Österreich, Kaiser *Franz Stephan*, dem Gatten der bekannten Kaiserin *Maria Theresia*, die grosse Sammlung des Florentiner Universalgelehrten *Johann von Baillou* angekauft wurde. Durch Aufsammlungen in den Ländern des damals sehr ausgedehnten österreichischen Kaiserreiches und durch vom Herrscherhaus grosszügig finanzierte Reisen nach Übersee wurden die in verschiedenen Teilen der Hofburg (der Residenz der österreichischen Kaiser) untergebrachten Sammlungen in den folgenden Jahrzehnten stark vergrössert und schliesslich auch in einer wissenschaftlichen Ordnung aufgestellt. Den drei Reichen der Natur entsprechend wurde eine Gliederung in drei "Kaiser-königliche Hof-Naturalienkabinett" vorgenommen. Diese entwickelten sich bald zu Zentren der naturwissenschaftlichen Forschung in Österreich und wurden trotz der immer drückender werdenden Raumnot durch weitere Aufsammlungen bereichert, beispielsweise durch einen langen Sammelaufenthalt (1817-1835) in Brasilien. Das Revolutionsjahr 1848 brachte einen schweren Verlust: im Verlauf der Kämpfe wurden grosse Teile der Zoologischen Sammlung durch einen Brand vernichtet, darunter auch die Lepidopteren-sammlung von *Schiffermiller* und *Denis*. Im Jahre 1889 konnte endlich der Raumnot durch die Eröffnung des neuen Naturhistorischen Museums auf der Ringstrasse gegenüber der Hofburg ein Ende bereitet werden, allerdings auch nur für einige Jahrzehnte, denn heute ist auch dieses grosse prächtige Gebäude bereits wieder zu klein geworden.

Die Lepidopterensammlung des Wiener Museums ist auch heute noch die grösste auf dem europäischen Festland. Sie umfasst ca. 2 Millionen Exemplare und zahlreiche, insbesondere auch alte, Typen.

Das Studium der Lepidopterologie hat in Österreich seit dem Ende des 18. Jahrhunderts eine rege Pflege erfahren. Im Jahre 1776 erschien das "Systematische Verzeichnis der Schmetterlinge der Wiener Gegend", herausgegeben von den Lehrern *Ignaz Schiffermüller* und *Michael Denis*. In diesem Buche wird zum erstenmal auf Grund der Kenntnis der Jugendstadien die von *Linné* geschaffene Anordnung der Lepidopteren abgeändert und so ein mehr natürliches System geschaffen. Das umfangreichste Werk über europäische Schmetterlinge in deutscher Sprache (17 Bände, 1807-1835), nämlich das von *Ferdinand Ochsenheimer* und *Friedrich Treitschke*, entstand vom 3. Band an ebenfalls in Wien, da beide Autoren am Wiener Burgtheater beschäftigt waren, ersterer als Schauspieler. Als Nachfolger *Treitschkes*, besonders auf dem Gebiet der Mikrolepidopteren, ist *Josef Fischer von Röslerstamm* (1787-1866) hervorzuheben, dessen Sammlung später an *Dr. Herrich-Schäffer* nach Regensburg verkauft wurde, der dadurch erst die Möglichkeit erhielt, sein Werk über europäische Schmetterlinge zum Abschluss zu bringen.

Der erste Lepidopterologe, der in den kaiserlichen Naturaliensammlungen (wie eingangs erwähnt, den Vorläufern des Naturhistorischen Museums) tätig war, nämlich als Kustos und später auch als Direktor des "Zoologischen Hofkabinettes", war *Vincenz Kollar* (1797-1860). Er veröffentlichte unter anderen auch Arbeiten, die fremdländische Faunengebiete betrafen, beispielsweise solche über Brasilien und Venezuela. Von besonderer Bedeutung für die Lepidopterensystematik waren die Arbeiten von *Julius Lederer* (1821-1870), dessen an Typen reiche Sammlung an *Dr. Staudinger* in Dresden (Deutschland) verkauft wurde. In Lepidopterenkreisen weit über die Grenzen Österreichs hinaus bekannt wurde auch der Name des Bürgermeisters von Wien *Cajetan Freiherr von Felder* (1814-1894). Neben Veröffentlichungen über verschiedene Tagfaltergruppen ist besonders die Bearbeitung der Lepidopteren aus den Ausbeuten von der österreichischen Weltumsegelung mit der Fregatte *Novara* (1857-1859) hervorzuheben. Seine Sammlungen kamen an *Sir Walther Rothschild* in dessen Privatmuseum nach Tring (England).

Der erste Kustos der Lepidopterensammlung am neu erbauten Naturhistorischen Museum war *Alois Rogenhofer* (1831-1897), neben dem durch 45 Jahre am Museum *Josef Mann* (1804-1889) als Präparator und insbesondere unermüdlicher Sammler wirkte; er beschrieb auch zahlreiche neue Arten, vor allem Mikrolepidopteren. Der Nachfolger *Rogenhofers* am Wiener Museum, Prof. Dr. *Hans Rebel* (1861-1940), war der bedeutendste Lepidopterologe Österreichs überhaupt. Von ihm stammen neben zahlreichen Neubeschreibungen aus den verschiedensten Familien der Gross- und Kleinschmetterlinge und anderen Arbeiten über Lepidopteren, der bekannte *Staudinger-Rebel*-Katalog der paläarktischen Lepidopteren und das im deutschen Sprachraum bei Liebhaberentomologen auch heute noch am weitesten verbreitete Schmetterlingswerk, nämlich die Neubearbeitung von *Berges* Schmetterlingsbuch, das zahlreiche Amateure zu einer wissenschaftlichen Betätigung mit Schmetterlingen anregte. Von solchen Sammlern stammt auch der grösste Teil des nach 1920 ans Wiener Museum gekommenen Schmetterlingsmaterials. Ein weiterer bekannter Lepidopterologe des Naturhistorischen Museums in Wien war Dr. *Hans Zerny* (1887-1945). Er unternahm zahlreiche Sammelreisen, unter anderen auch eine nach Südamerika. Sein Spezialgebiet waren die Syntomiden. Nach seinem Tod war die Schmetterlingssammlung des Wiener Museums bedauerlicherweise durch 15 Jahre nicht mit einem Lepidopterologen besetzt. 1960, also im Jahre des 11. Internationalen Kongresses für Entomologie, der damals in Wien stattfand, wurde sie dem Verfasser dieser Zeilen anvertraut. Leider muss festgestellt werden, dass heute die Ausstattung des Naturhistorischen Museums in Wien mit Personal und finanziellen Mitteln in keinem angemessenen Verhältnis zu der Grösse und der wissenschaftlichen Bedeutung seiner Sammlungen steht, was nur zum Teil durch die geringe Grösse des heutigen österreichischen Staates zu entschuldigen ist.

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NOTICE

THE PRECEDING PAPER by Dr. Fritz Kasy is the first of what the editor hopes will be a series devoted to institutions which have in the past and present spent much effort in furthering the knowledge of the Lepidoptera, not only in the amassing of collections but also in the constructive work in the field of experimental research. It is by means of the latter mentioned experimental work that the systematic work of the museums and private collectors can best be understood and appreciated.

It is hoped that present workers in such institutions will feel free to send historical papers to implement this series.

William Hovanitz

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HABITAT: ADELA BELLA IN FLORIDA (INCURVARIIDAE: ADELINAE)¹

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Little is known of the biologies of adelid moths and the life history of *Adela bella* Chambers, in particular, is unknown. While beginning studies of the moth in March 1973 at Torreya State Park in the panhandle of Florida, males were found to congregate on the leaves of *Carpinus caroliniana* (Betulaceae) trees deep in the deciduous forest on the slopes overlooking the Apalachicola River (females were not found). Male congregations by adelid moths, however, do not necessarily indicate the oviposition host.

The illustration of the forest at Torreya State Park shows *Carpinus* mixed in with other deciduous trees and generally shows the shaded habitat in which *A. bella* may be encountered. The *Carpinus* leaves from which males were taken is in the upper foreground left and closest to the viewer near the top of the picture. The moth is diurnal like other adelids and is widely distributed in the eastern United States and Canada, occurring mainly in the Appalachian Mountains in the South. There have been other records of *A. bella* in Florida but the species is well established in this Apalachicola uplift at Torreya State Park which is ecologically similar to the southern Appalachians of northern Georgia and Alabama.

Males fly in a bouncing but slow fashion on sunny days (mid-March to mid-April in Florida), their long antennae held upwards. Moths are encountered flying or resting on *Carpinus* and other leaves and also near flowers.

¹Florida Agricultural Experiment Station Journal Series No. 5308.

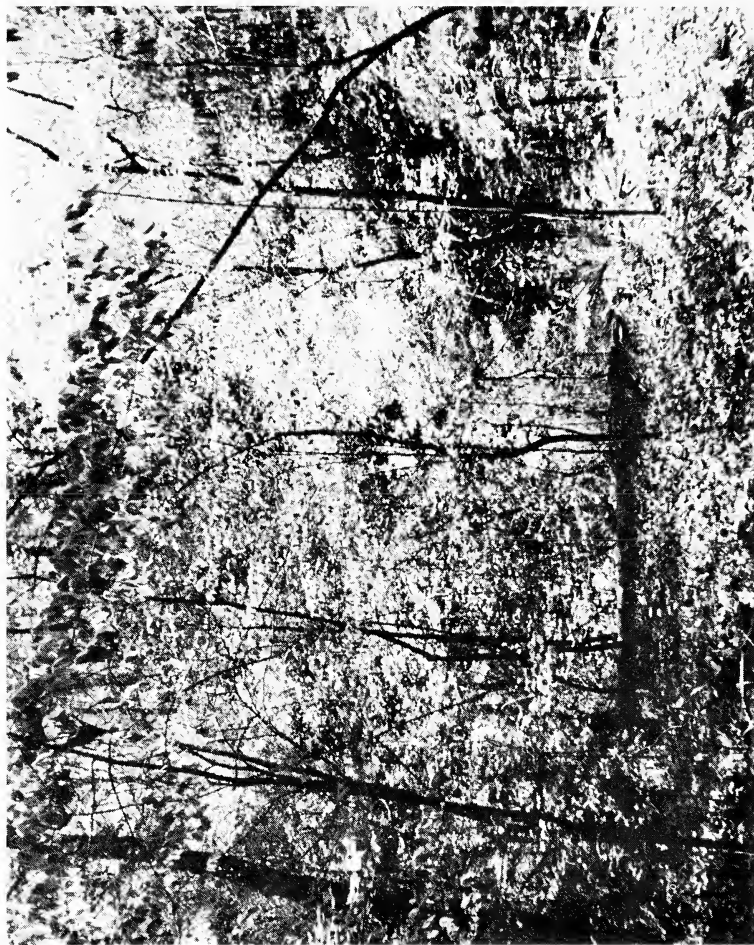


Fig. 1.—Deciduous forest habitat of *Adela bella* at Torreya State Park, Liberty Co., Florida. (19 Mar 1973)

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

CONTENTS

<i>Volume 12</i>	<i>Number 1</i>	<i>March, 1973</i>	
A new species of <i>Papilio</i> from the eastern United States (Papilionidae)	J. Richard Heitzman	1	
Specific entities of the subgenus <i>Icaricia</i> Nabokov (Lycaenidae)	J. W. Tilden	11	
The correct name for the subspecies of <i>Limenitis weidemeyerii</i> occurring in Arizona (Nymphalidae)	Cyril F. Dos Passos	21	
A review of carrying pair behavior and mating times in butterflies	Oakley Shields and John F. Emmel	25	
<i>Volume 12</i>	<i>Number 2</i>	<i>June, 1973</i>	
The ecological associations of the butterflies of Staten Island	Arthur M. Shapiro and Adrienne R. Shapiro	65	
<i>Volume 12</i>	<i>Number 3</i>	<i>September, 1973(1974)</i>	
On the origin of austral elements in the moth fauna of south-eastern Ontario, including a number of species new for Canada R. Harmsen, P. D. N. Hebert and P. S. Ward		127	
The study of populations of Lepidoptera by Capture-Recapture methods P. M. Sheppard and J. A. Bishop		135	
Life history studies of <i>Idaea obfusaria</i> (Walker) Roger L. Heitzman		145	

Survey of ultraviolet reflectance of Nearctic butterflies	James A. Scott	151
Butterflies of St. Croix	Charles F. Leck	161
An improved method for rearing the Monarch butterfly	Charles Munger	163
An annotated checklist of the Missouri Geometridae	Roger L. Heitzman	169
Cover Illustration: Variation in <i>Colias nastes</i> of Lapland	William Hovanitz	180
Volume 12	Number 4	December, 1973 (1974)
Adult behavior and population biology of two skippers mating in contrasting topographic sites	James A. Scott	181
Acceptance of artificial diet by <i>Megathymus streckeri</i> (Skinner)	M. A. Petterson and R. S. Wielgus	197
Some observations on the eggs of moths and certain aspects of first instar larval behavior	Noel McFarland	199
New food plant for <i>Darapsa pholus</i> (Cramer)	J. C. E. Riotte	209
The nomenclature in an important British check list (1972). Part I.	Juraj Paclt	211
A name for <i>Glaucopsyche lygdamus</i> auct., not Edwards 1862.	J. W. Tilden	213
Junonia and Precis. A correction.	J. W. Tilden	216
The flight periods of several sibling species of moths.	Charles L. Selman	217
Lifespan of Butterflies	James A. Scott	225
Altitudinal migration of butterflies in the central Sierra Nevada	Arthur M. Shapiro	231
Early stages and biology of <i>Phyciodes orseis</i> .	James A. Scott	236
Book Review: Annotated check list of the butterflies of Illinois by R. R. Irwin and J. C. Downey	R. S. Funk	243

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Need aid in preparation of specimens for study of population structure in butterflies; involves obtaining population samples, mounting, laboratory breeding, etc. Full or part time. Contact William Hovanitz, 1160 W. Orange Grove Ave. Arcadia, Calif. 91006.

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

Volume 13

Number 1

March, 1974

IN THIS ISSUE

- Studies on Nearctic *Euchloe* — Part 7
Paul A. Opler 1
- 3 Stacks of the eggs of *Hemistola* hatching
Noel McFarland 21
- Checklist of the Macroheterocera of
south-eastern Ontario
P. S. Ward, R. Harmsen, and P. D. N. Hebert 23
- A new species of *Hypagyrtis*
Roger L. Heitzman 43
- Genetic control of maculation and
hindwing color in *Apantesis phalerata*
Jack S. Bacheler and Thomas C. Emmel 49
- Natural and laboratory occurrence of "Elymi"
phenotypes in *Cynthia cardui* (Nymphalidae)
Arthur M. Shapiro 57
- Das naturhistorische Museum in Wien
und seine Lepidopterensammlung
Dr. Fritz Kasy 63
- Notice
William Hovanitz 66
- Habitat: *Adela bella* in Florida
John B. Heppner 67

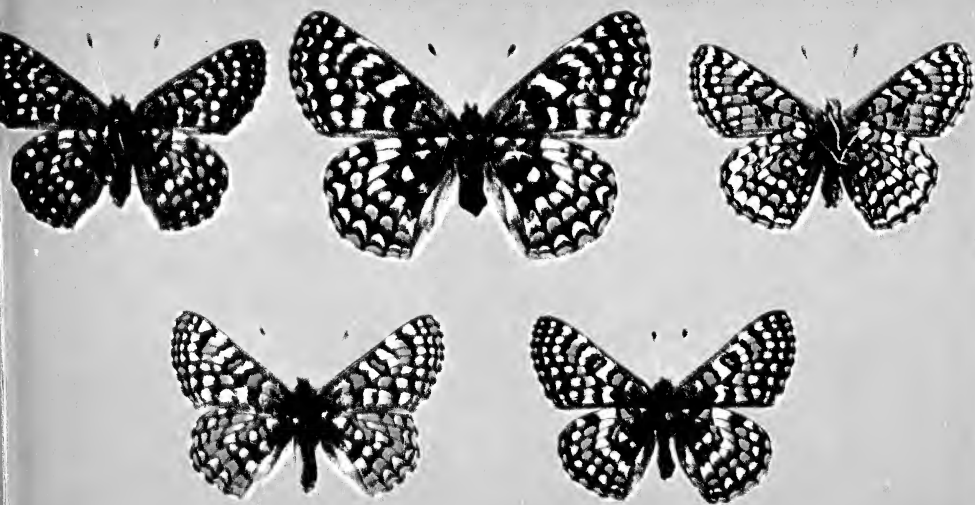
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OF RESEARCH
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THE BUTTERFLY FAUNA OF THE SACRAMENTO VALLEY, CALIFORNIA

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INTRODUCTION

THE STATE OF CALIFORNIA has an extremely rich and varied butterfly fauna, reflecting its topographic, climatic, and botanical diversity (Comstock, 1927; Munz, 1970; Bakker, 1971). The montane faunas, which are perhaps best known, are characterized by a high proportion of endemic species and subspecies. In recent years regional faunas have been published for Sierra Nevada localities: Yosemite National Park (Garth and Tilden, 1963), Mather (Shields, 1966), and Donner Pass (Emmel and Emmel, 1962). A study by Opler and Langston (1968) included both Outer and Inner Coast Ranges in Contra Costa County, as well as part of the Sacramento-San Joaquin Delta. The least well-known butterfly fauna in northern and central California is that of the rather densely populated Sacramento Valley (fig. 1). This is scarcely surprising when the current biotic condition of the Valley is considered. The following discussion is drawn primarily from Thompson (1961) and Sculley (1973), who discussed the climatic, physiographic, and ecological conditions of the pristine and present Valley.

VEGETATION

The vegetation of the Sacramento Valley has been more thoroughly modified by man than that of scarcely any comparably large area in North America. Prior to European-American colonization, three natural communities were widespread in the Valley: bunchgrass-Valley Oak savanna; tule-cattail marsh; and riparian forest (fig. 2). Perennial bunchgrass, with scattered groves of Valley Oak (*Quercus lobata* Nee.), occurred on the higher sites not subject to regular flooding, and was the com-

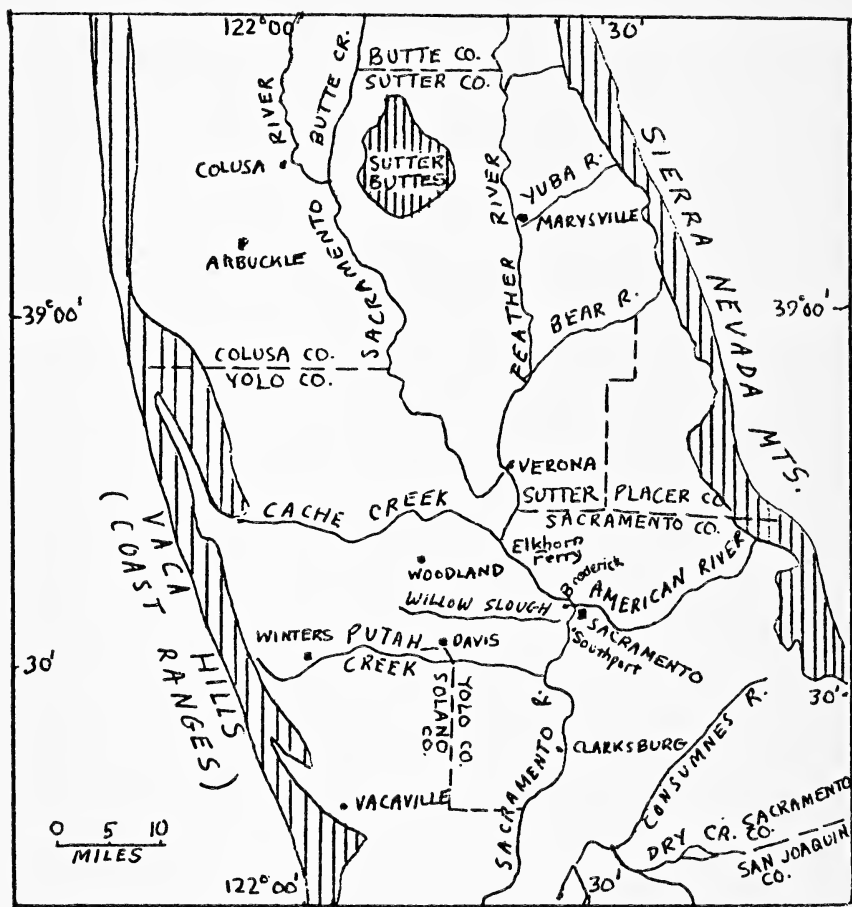
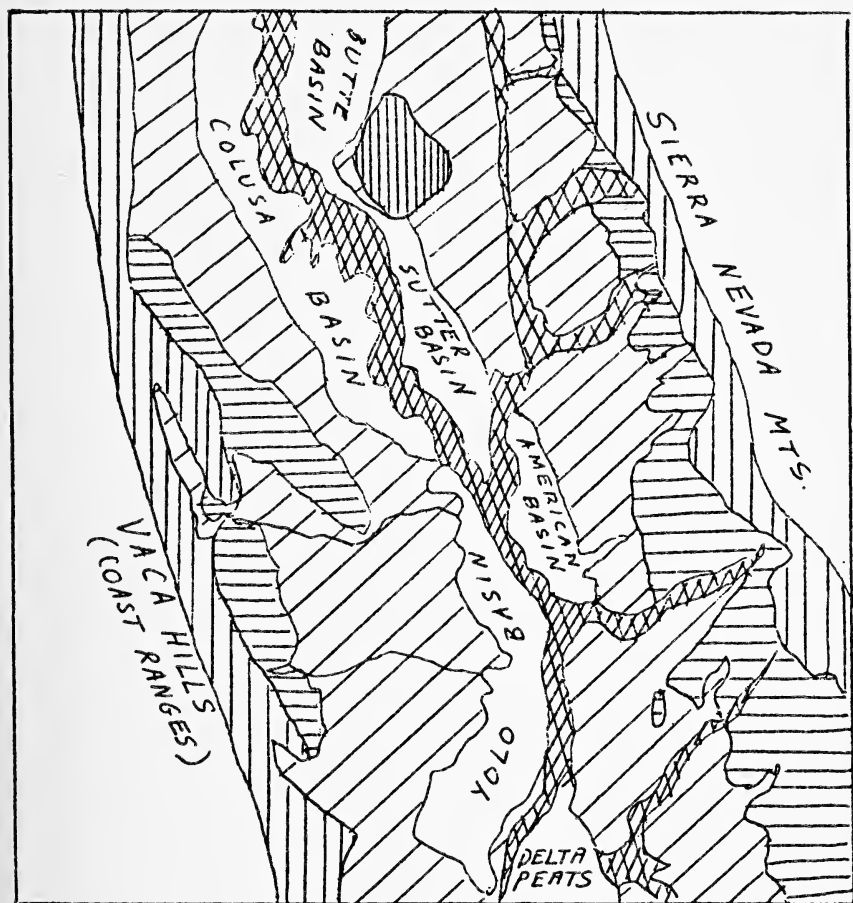


Fig. 1.—Location map of the central Sacramento Valley.



UPLANDS -
MOSTLY CHAPARRAL

RED LANDS OR
OLD ALLUVIUM -
OAK & GRASS

ALLUVIAL PLAINS -
FORMERLY SAVANNA

RIPIARIAN
FOREST &
"NATURAL LEVEES"

BASIN FLOOD BASINS -
FORMERLY TULE
MARSHES

Fig. 2.—Physiographic subdivisions of the central Sacramento Valley, with present biotic communities.

monest vegetation type in the Valley, especially on the west side. The lowlands, which were inundated in normal winters (and in wet years well into summer), supported vast areas of cattails (*Typha*) and common tule (*Scirpus acutus* Muhl.). Torrential rains on the Sierran west slope fed the periodic overflows of the Sacramento River and its tributaries. The major streams built up "natural levees" of silt deposited during flood stages, and these supported a lush deciduous forest dominated by Fremont Cottonwood (*Populus fremontii* Wats.). Deciduousness in a Mediterranean climate like that of California is a luxury which can be afforded only when a reliable year-round supply of ground water is available. The riparian forests of the Sacramento Valley were unique at low elevation in the state.

Of the first two communities little or nothing remains. Most of the bunchgrass prairie was put into pasture or under the plow; either way, the native bunchgrasses were competed out of existence by introduced annual grasses, mostly from Europe. With the bunchgrasses most of the native flora, both annual and perennial, also succumbed, to be replaced by weedy Crucifers, Borages, Mallows, Composites, and other aliens. The marshes were diked or drained and reclaimed for agriculture, or else grossly modified as overflow channels for flood control (the Yolo, Colusa, and Sutter Bypasses). Their original character has in most places been lost. Relict marshlands still exist in West Sacramento and south of Sacramento, at Beach Lake and Stone Lake. Substantial fragments of riparian forest remain in public and private hands—more or less modified by the deletion of native species and the addition of weedy ones, and by restriction in most places to the immediate riverbank where they once had reached 1-4 miles inland.

Little of the Sacramento Valley is free of major ecological disturbance for any significant length of time, and except for the creek bottoms the successional potential of the area—with its radically altered flora—is not really predictable. Most of the former bunchgrass-oak savanna is either intensively farmed or urbanized. The lowland basins are farmed, or farmed in summer and flooded in winter. The riparian forests are under increasing recreational-use pressure, especially from off-road vehicles.

To a casual visitor, the Valley presents a monotonous vegetation due to the ubiquity of early-successional, adventive species. These broadly adapted plants tend to obscure soil and water-table differences which do, however, become apparent in

more mature stands. The lack of native plants and major topographic features, and the constant presence of man tend to discourage butterflies (and Lepidopterists as well). The sandy American River lowland in Sacramento County is mostly not in agricultural use and has the richest butterfly fauna in the Valley, as well as the most mesic vegetation. Thirty-six species—58% of the total Valley fauna—were recorded flying there on June 2, 1973, and the total number of species ever recorded there is 53, or 85% of the Valley fauna. Nonetheless, most of the species are highly vagile and occur in foothill canyons on both sides of the Valley; there is little to necessitate postulating a relict (pre-American) origin for any of the present butterfly populations in the Valley (except perhaps *Phyciodes campestris*).

CLIMATE AND BUTTERFLY PHENOLOGY

Sixty-two species of butterflies have been recorded in the Valley. This is a fairly small fauna by California standards; 134 species are recorded in Yosemite, 84 in Contra Costa County, 74 at Mather (Tuolumne County), about 80 at Donner Pass (Placer County), 70 at Boreal Ridge and 63 at Marin-Sierra Camp, both Nevada County (Shapiro, unpubl.), and about 65 in the east-slope canyons of the Vaca Hills immediately west of the valley (data in part from Shields, pers. comm.). When species which fly into or through the Valley but are not known to breed there are excluded, the fauna drops to 53.

This fauna contrasts strikingly with others in California in the distribution of voltinism. In climates where rainfall is relatively evenly distributed through the year, the proportion of univoltine species increases steadily with elevation and with the shortening of the growing season. In California the summer drought is reflected in the widespread evolution of vernal univoltinism in butterflies at low elevations. The low proportion of univoltines in the Sacramento Valley—only 13% of the resident species (as compared with 39% of the species in the nearby Vaca Hills, Table 1)—reflects the reliable supply of summer water associated with the riparian systems and agricultural irrigation. It also reflects the origins of the fauna, which is largely recruited from the riparian lands where the summer drought has always been less severe than elsewhere.

Relatively few California butterflies are facultatively univoltine; species with only a single brood anywhere generally have only one everywhere, despite considerable altitudinal ranges.

Species which are flexible in brood sequence are primarily lowland colonizers which periodically invade higher elevations but cannot be considered permanent residents there: *Vanessa* spp., *Precis coenia*, *Strymon melinus*, *Lycaena helloides*, *Plebeius acmon*, *Pieris rapae*, *P. protodice*, *Colias eurytheme*, *Pyrgus communis*, *Hylephila phylaeus*. These species are adapted to temporarily unstable habitats, and whatever their geographic origins their seasonal cycles have probably always included up- and downslope colonization. They are the most conspicuous element of the Valley fauna, where they disperse from one disturbed habitat to another in response to agricultural practices. In good years Valley populations probably serve as a source for colonizers which reach the high Sierra.

The climatology of the Sacramento Valley is unusually well documented for the Far West. Reliable records at Sacramento extend back to 1849-50, and recent compilation of means and extremes has been prepared (Figgins, 1971). The Valley has a Mediterranean climate in which rainfall occurs from September to April and is usually concentrated in December, January, and February (see Tables 2 and 3). The Coast Ranges insulate much of the Valley from direct maritime influence and the resulting continentality is shown in the high summer maxima and occasionally low winter minima. The gap in the Coast Ranges at the Carquinez Straits allows a shallow penetration of maritime air in summer which terminates periods of extreme heat after two to four days. Skies are clear in summer, but widespread and persistent low cloudiness and fog prevail in winter and are especially heavy in and near the river bottoms. The highest summer temperatures and the clearest, driest winter weather are provided by "northers," strong northerly winds which develop in response to a north-south pressure gradient and are warmed and dried by their descent from the Siskiyou.

WINTER AND DIAPAUSE STRATEGIES

Sacramento Valley winters are mild and essentially snowless except in the extreme north. Freezes occur up to 30 times each winter, but temperatures below 25°F and continuous freezes of longer than ten hours are exceedingly rare. Under these conditions non-diapausing butterfly immatures may continue their development through the winter. Larvae of *Pieris rapae* from eggs laid in late November develop slowly to pupation in late January at Davis and Woodland. The resulting pupae enter

diapause and eclose in late March or April. Diapausing pupae formed in December or earlier eclose in February and March. A similar winter history is reported for *P. rapae* in England (Gardiner, 1972).

Diapause is generally considered an adaptation to cold winters, and indeed is associated with biochemical defenses against intracellular and extracellular freezing. But in both cold- and mild-winter areas it serves as a timing mechanism correlating spring emergence with the onset of weather suitable for adult activities and—most importantly—likely to be sustained. The limiting factor on butterfly breeding in winter in the Sacramento Valley is the unsuitability of overcast, humid weather for flight activity, regardless of temperature. Persistent fog and low overcast initiate winter in the Valley while temperatures are still relatively high. Winter emergences of Pierid butterflies during fair, mild periods are less common than in the northeastern United States. Spring emergences coincide with decreasing cloudiness and humidity in February and March, and a temperature regime comparable to that in the emergence seasons of the same species in cold-winter areas. Availability of suitable flight weather, rather than nectar sources, seems to be the predominant factor here; major blooms of nectar-rich plants, some native, begin in January in dry years and may continue all winter in wet ones.

The flight season begins several days to two weeks later in the Valley than in the canyons of the Vacas (up to 500 feet). These canyons are sheltered from the spring “northers” which render many otherwise suitable days in the Valley unfit for flight. They also have less fog and dew (which cools the air near the ground and may prevent flight activity most or all of the day if the ambient humidity stays high). The topography of the Valley floor itself also has a bearing on flight times. The American River bottomlands become damp and foggy earlier in fall than the higher ground, and flight activity there ends earlier as a result. During the winter temperatures are moderated by the rapidity with which the air is saturated, and wind velocities (and the desiccating effects of “northers”) are braked by the forest cover. Most species emerge four to twelve days earlier in spring at the American River than elsewhere. The local climate there allows *Pieris protodice* to overwinter reliably, something it does only very sporadically in the Valley.

One ecological consequence of the dominance of adventive weeds is the absence of all but a handful of butterfly species

from very extensive tracts of agricultural land. Only one of these is itself adventive from Europe, *Pieris rapae*. Under Valley conditions *rapae* and its primary hosts, *Brassica* spp., are not well-coordinated seasonally. Weedy mustards behave as winter annuals, seldom sustaining much frost damage, and are past their prime when the spring brood of *P. rapae* is peaking. The phenology of alfalfa (*Medicago sativa* L.), the major host of the Orange Sulphur, *Colias eurytheme*, is similar to that of the native perennial legumes on which this butterfly originally fed. *C. eurytheme* overwinters as a third- or fourth-instar dormant (diapausing?) larva.

Hibernating Nymphalid adults generally do not fly on the 10-20 potentially suitable days in winter; they appear in February just before the non-hibernating butterflies. The energetics of Nymphalid hibernation in the mild Sacramento Valley winter is of considerable interest, especially in the Mourning Cloak (*Nymphalis antiopa*) which disappears in early August and remains dormant for six months. Its failure to rear a second brood even along the major rivers is rather perplexing. *Vanessa* (= *Cynthia*) *annabella* departs from the usual pattern of its relatives by overwintering largely as pupae formed in December and early January. Adults alive in December also hibernate successfully, and fresh adults may eclose during warm spells in winter and enter hibernation. This species has been recorded flying 50 weeks of the year at Davis and is the closest thing to a year-round breeder in the Valley. In 1973, when it was abundant, *V. cardui* also bred well into December and continued to eclose.

RAINFALL AND INTERSEASONAL VARIANCE

One of the most striking aspects of Valley climatology is the very high interseasonal variance in rainfall. Temperature characteristics are less variable. Some idea of the variance in precipitation may be obtained from figure 3 and Table 3. The uncertainty of rainfall would be expected to produce adaptations for facultative diapause in species whose host plants are rainfall-dependent. The Papilionid *Battus philenor* produces some diapause pupae in all broods, regardless of photoperiod; these eclose the following spring (rarely fall), with no apparent chilling requirement. *B. philenor* is primarily a foothill species, breeding in canyons where the host plant grows along intermittent

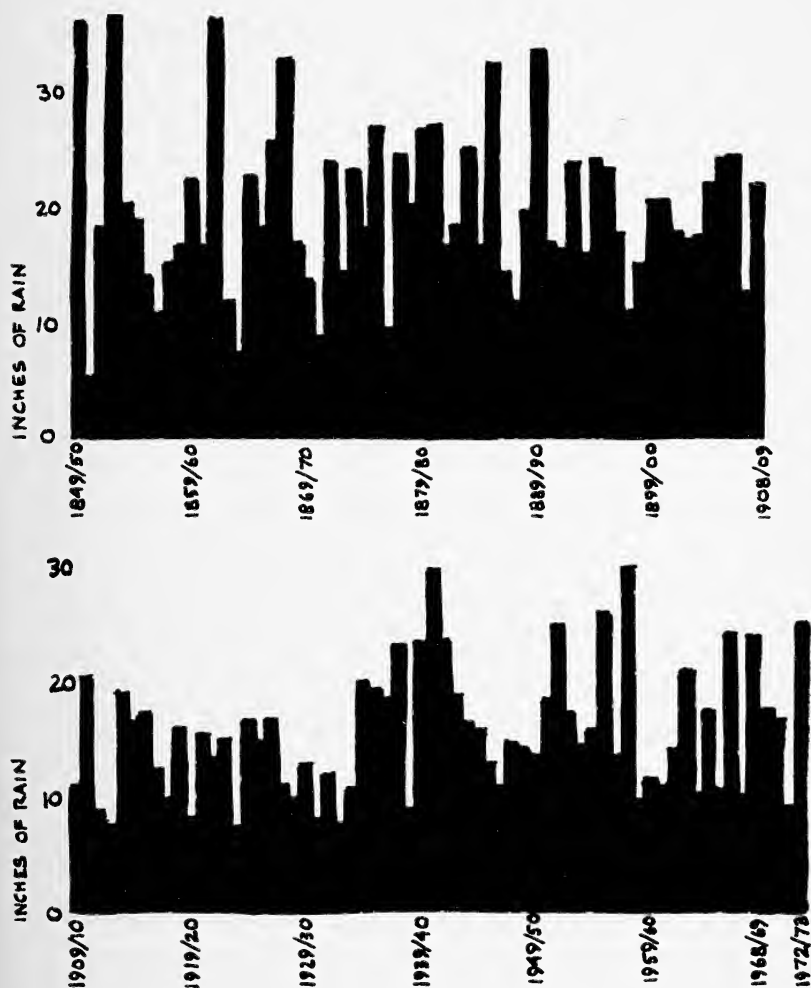


Fig. 3.—Total seasonal rainfall at Sacramento, 1849/50 through 1968/69. From Figgins, 1971.

streams. A similarly mixed developmental strategy occurs in *Euchloe ausonides* and *Anthocharis sara* in the foothills and may be an adaptation to interseasonal variance in rainfall itself, rather than stream flow. On the Sacramento Valley floor, *B. philenor* and *A. sara* are both locally single-brooded, but *E. ausonides* is double-brooded. There is preliminary evidence to suggest that the Davis population of *B. philenor* is genetically univoltine, perhaps reflecting founder effect—sampling error introducing only a portion of the variability of a polymorphic source population.

Dates of spring flights in both univoltine and multivoltine butterflies are well known to be related to weather conditions, both during the emergence season and during the preceding winter. In the Valley, first-flight dates are less variable than in either the Sierra Nevada or upstate New York, both cold-winter areas (cf. Shapiro, 1974a). Even so, dates for the first species, e.g. *Pieris rapae*, may vary several weeks among seasons. Precipitation advances the condition of the vegetation, but overwintering larvae and pupae respond to temperature and perhaps photoperiod. Table 4 presents first-flight dates for 25 common spring butterflies in the Valley after the very dry but mild 1971-72 and very wet and cold 1972-73 winters. Weather data for the two seasons appears in Table 5 and may be compared with the norms in Tables 2 and 3. Although the 1973 flight season began early, continuing episodes of wet and windy weather delayed most species relative to 1972. Emergences in the Vaca canyons were earlier than in the Valley and showed much less departure from 1972 dates, although population levels of many species were quite different in the two years.

Later-emerging species are increasingly insensitive to weather as a determinant of first-flight date. *Satyrium sylvinus*, for example, first appeared v.10 in the Valley in 1973 as against v.15 in 1972 (v.8.72 in the Vacas), but its period of peak numbers was the same both years.

Cutoff dates for flight in autumn are also under meteorological control for the highly multivoltine species. An especially sensitive species is *Papilio zelicaon*. In 1972 it was last recorded on ix.20; in 1973 a full month later, on x.30. That this discrepancy reflects a seasonal difference is well illustrated by data on this species at Suisun Bay, near Fairfield, where the climate is more maritime and *P. zelicaon* normally flies later; in 1972 it was last seen on xi.5 and in 1973 on xi.18.

(Continued on page 115)

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EXTENDED FLIGHT PERIODS OF COASTAL AND DUNE BUTTERFLIES IN CALIFORNIA¹

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SEVERAL OF THE RHOPALOCERA that occur close to the Pacific Ocean in California have very long flight periods, giving the appearance of more than a single generation per year. Further inland these same species (often a differently named subspecies), have shorter flight periods, leaving no doubt of their being univoltine.

To illustrate, I have chosen ten examples scattered among the families Pieridae, Nymphalidae, Riodinidae, Lycaenidae and Hesperiidae. In each case, one or two examples of the coastal populations are treated. These are then compared directly with populations further inland. "Inland" in some cases, may be only 20 miles or so away from the coast—if examples are available from the middle and inner Coast Ranges. In other cases, the comparisons are made with the West Slope, High, or East Slope of the Sierra Nevada.

Figures 1 and 2 name the coastal populations in capital letters, and those inland in lower case. The flight periods based on known records are shown within the bars—black for coastal populations and stippled for inland. The diagonal lines at one or both ends of most bars show the probable extensions of the flight periods based on: 1) Abundance at the beginning or end of the known collections; and 2) Fresh and/or worn specimens at the known beginning or end.

Although more ♂♂ are usually present at the beginning, and more ♀♀ toward the end of the various flight periods, in general both sexes were present throughout most of the coastal flights. Since no *Speyeria*, *Cercyonis* or *Erebia* are involved in this study, any staggered appearance of the sexes is considered negligible.

¹Presented at the Twentieth Annual Meeting of the Lepidopterists' Society, Pacific Slope Section, Santa Barbara, Calif., 25 Aug. 1973.

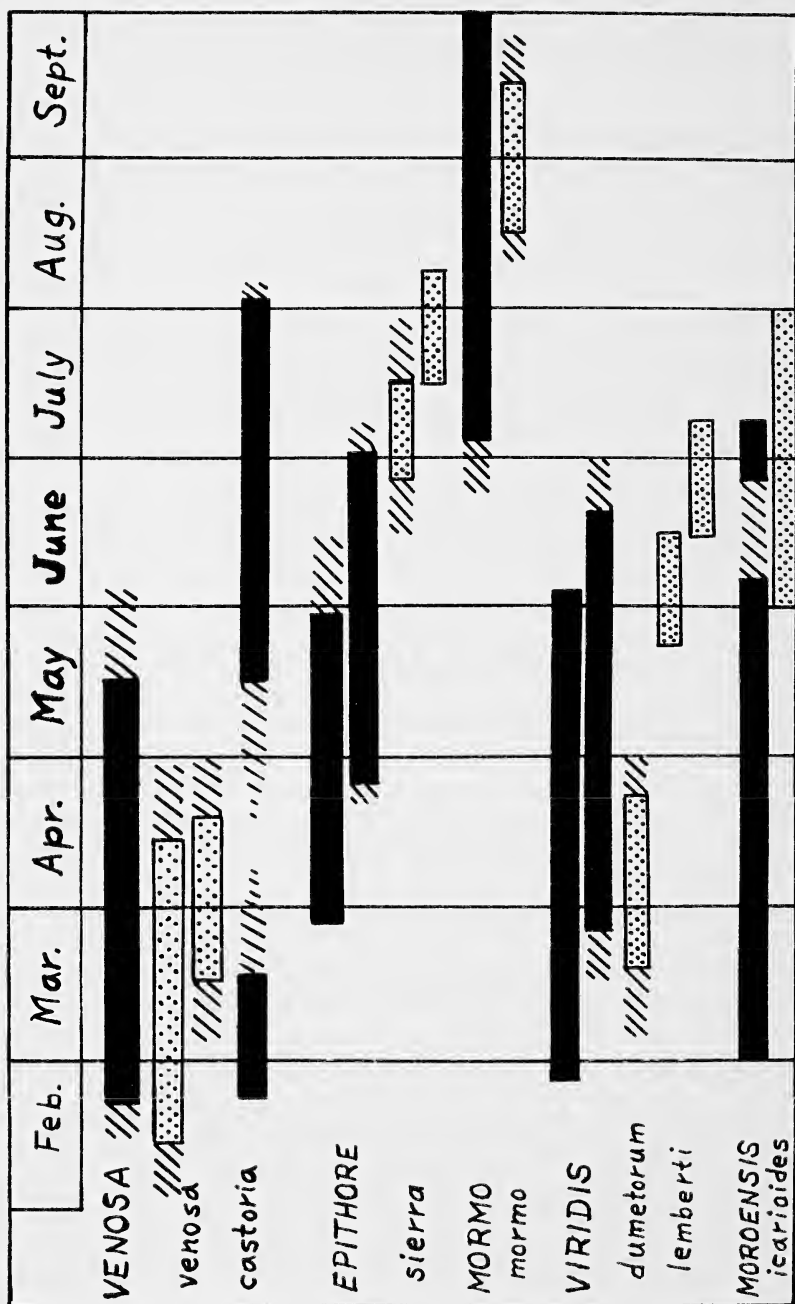


Fig. 1.—Flight periods of coastal populations (solid) and inland (stippled). Diagonal lines indicate possible extensions of seasons.

The most exact measurements of flight periods are the cases where there are sufficient records for a single season at the same locality. This data was used whenever possible. However, from my own records, and the data from several publications, it appears that most lepidopterists only visit the same location once or twice in a single season. Hence, the other records are based on the extremes of several seasons from data already published, or on the labels of the specimens. Experienced collectors tend to time their visits to obtain fresh "mint" specimens. For a study of this type, it would be advantageous for the collectors to also go after worn examples, or at least record them in field notes. Partly because of lack of worn examples, I have extended the probable seasons of some populations to later dates.

Pieris napi venosa Scudder

At Partington Canyon south of Big Sur in coastal Monterey County, fresh specimens of both sexes were taken on 21 Feb. 1965. Other examples were taken various seasons in March, April and May. My latest date is 15 May 1966—some worn, but several also fresh. Therefore, the season for the "true" heavily-veined *venosa* would probably extend another three weeks—into June (diagonal lines in Fig. 1).

Further inland in the Coast Ranges (Alum Rock Park, Santa Clara County; Stonybrook Canyon & Redwood Canyon, Alameda County; and even as far inland as Thompson Canyon, Yolo County) my personal records extend from mid-Feb. to mid-April. This is a combination of many seasons, and the flight period is considerably shorter than on the coast. Inland examples become smaller and have less dark scaling on the veins. Many grade into the taxon *microstriata* Comstock, relegated to a synonym of *venosa* in dos Passos (1964).

Even further inland (West Slopes of the Sierra Nevada), I have recorded it at the lower elevations from mid-March to mid-April. This is based on fewer records, so I will give it the benefit of the doubt and extend the season considerably at both ends.

Status of gen. aest. *castoria* Reakirt: Although stated in the literature (Comstock, 1927; Tilden, 1965) that this is the second brood of *venosa*, there is still some doubt. Many places where I have found *venosa* commonly, I never found any *castoria*. In fact, in my experience, *castoria* is a rather rare entity.

On the other hand, *castoria* has been found flying with the heavily-veined *venosa*. Dennis Sorg (in his 1971 Season Summary contribution) found the two together as early as 20 March 1971 near Jasper Ridge, San Mateo County. I have not seen these

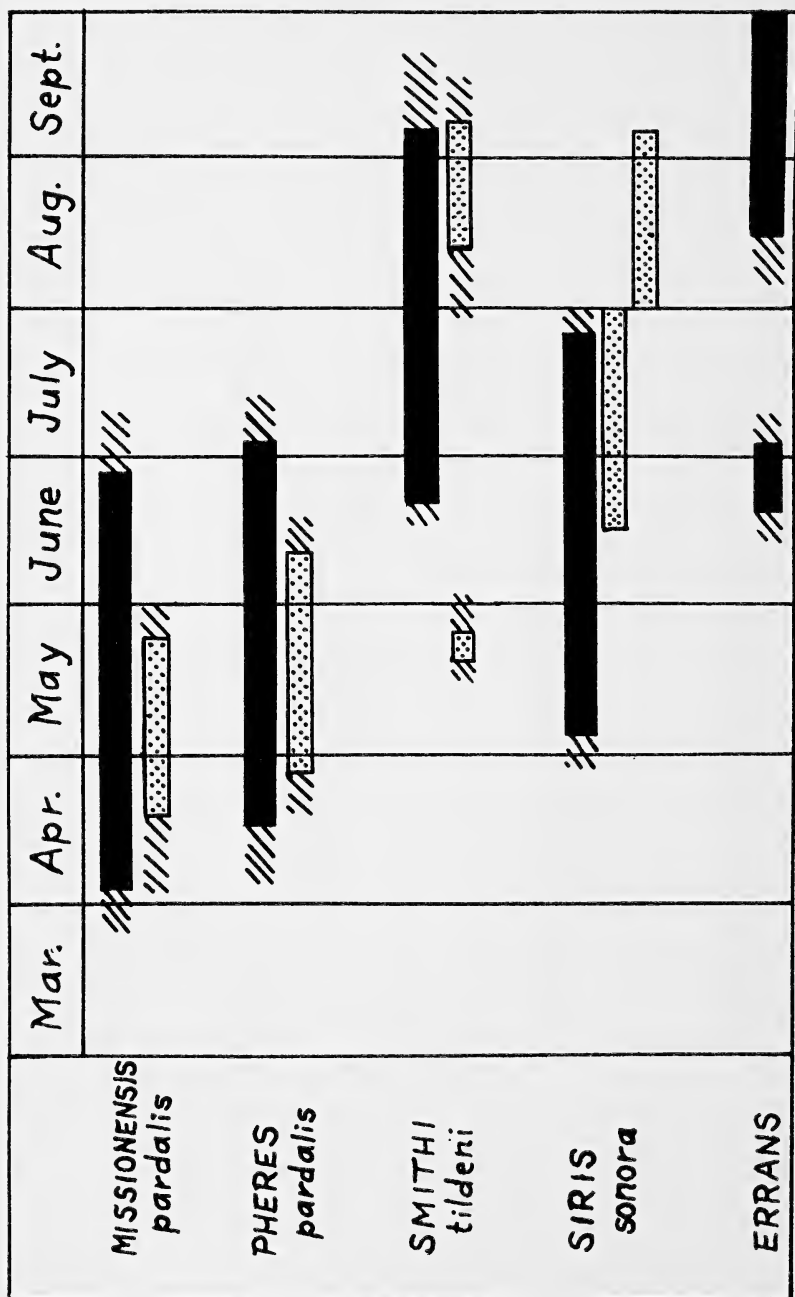


Fig. 2.—Flight periods of coastal populations (solid) and inland (stippled).
Diagonal lines indicate possible extensions of seasons.

specimens. On 15 May 1966, I found *castoria* flying with fresh *venosa* at Partington Canyon. Would these actually be the second brood from those flying in February and March? If not a separate species, why are there still fresh *venosa* phenotypes present at the same time?

The season on Fig. 1 for *castoria* is probably too long, as it represents all of my records from south to north on the coast. The mid-May record compares directly as it is also Partington Canyon, and there are other records on into late June in the Big Sur area (Bruce Walsh, correspondence). The extension of the bar into August is based on a single ♀ from Van Damme Park on the Mendocino County coast. Therefore, the season is probably somewhat shorter at any single location.

Boloria epithore epithore (Edwards)

The upper black bar represents the one season of 1970 on the Mendocino County coast. The earliest date is mine of 28 March 1970 at Russian Gulch State Park. On 30 May 1970 it was also taken near Russian Gulch by John Emmel and several on the same date near Caspar Beach by Paul Opler. With some fresh and others worn, this single season probably extended well into June. All of this data is cited in Perkins & Meyer (1973). Some examples from north-coastal California are assignable to *B. epithore chermocki* Perkins & Perkins (see Fig. 3).

The lower black bar represents *epithore* in the Santa Cruz Mountains. Most dates are in May and June, but some in different years include late April to the first of July (Perkins & Meyer, 1973). Since this represents many seasons from the 1890's to the present, I cannot extend it much on either end for a single season.

The stippled bars denote *Boloria epithore sierra* Perkins & Meyer. The upper one represents four seasons I collected along the North Fork of the Stanislaus River, Calaveras and Tuolumne Counties. Worn examples were found in late June, 1973 at slightly above 5000 ft. I did not take it that low in the other seasons as it no doubt had already flown. The other seasons it was considerably higher—almost 7000 ft. at Wet Meadow (ridge to the south) or at Big Meadows along Highway 4 (to the north). Therefore, it is in abundance for only about two weeks at any one spot, and the season is only a little over a month—even taking into consideration an almost 2000 foot range in elevation. The lower bar denotes an even higher elevation (Tioga Pass, Tuolumne Co.) where it extends from mid-July to early August (Perkins & Meyer, 1973).

Fig. 3.—Examples from coastal populations. Most localities in California, unless otherwise noted.

Row 1.—*Pieris napi venosa*: Partington Canyon, 9 mi. S. of Big Sur, Monterey Co., ♂, ♀ 21 Feb. 1965, RLL. *Boloria epithore chermocki*: Russian Gulch, Hwy. 1, Mendocino Co., ♂ 28 Mar. 1970, RLL. *B. e. epithore*: Santa Cruz Mts., Santa Cruz Co., ♂ 15 June 1946, T. W. Davies — CAS. All following specimens leg. R. L. Langston.

Row 2.—*Apodemia mormo mormo*: Dunes W. of Seaside, Monterey Co., ♂ 4 Sept. 1969; ♀ 19 Aug. 1963. *Callophrys viridis*: San Bruno Mts., San Mateo Co., ♂ 30 Mar. 1968; Point Reyes dunes, Marin Co., ♀ 25 Apr. 1970; Fort Baker, S. of Sausalito, Marin Co., ♀ 7 Mar. 1970.

Row 3.—*Callophrys viridis*: Marina Beach dunes, Monterey Co., ♂ 11 May 1969; ♂ 16 Apr. 1973. *Plebejus icarioides moroensis*: Dunes nr. Oso Flaco Lake, 5 mi. S. of Oceano, San Luis Obispo Co., ♂ 6 June 1966; ♂ 18 Apr. 1973; ♀ 6 June 1966.

Row 4.—*P. i. missionensis*: San Bruno Mts., San Mateo Co., ♀ 2 Apr. 1972; Twin Peaks, San Francisco, ♂ TOPOTYPE, 10 Apr. 1954; ♀ TOPOTYPE, 15 May 1954; *Plebejus pheres*: Point Reyes dunes, Marin Co., ♂ 25 Apr. 1970, ♀ 10 May 1973.

Row 5.—*Philotes enoptes smithi*: Dunes W. of Seaside, Monterey Co., ♂ 24 Aug. 1962; ♀ 26 Aug. 1971; ♀ 4 Sept. 1969. *Polites sonora siris*: 3 mi. W. of Plantation, Sonoma Co., ♂ 5 May 1955; ♀ 23 July 1955.

Row 6.—*P. s. siris*: Lake Sylvia, Grays Harbor Co., Wash., ♂, ♀ 4 July 1958. *Panoquina panoquinoides errans*: Mouth of Ventura River, Ventura Co., ♂, ♀ 30 Aug. 1971; 1 mi. S. of Solana Beach, San Diego Co., ♂ 1 Sept. 1971.

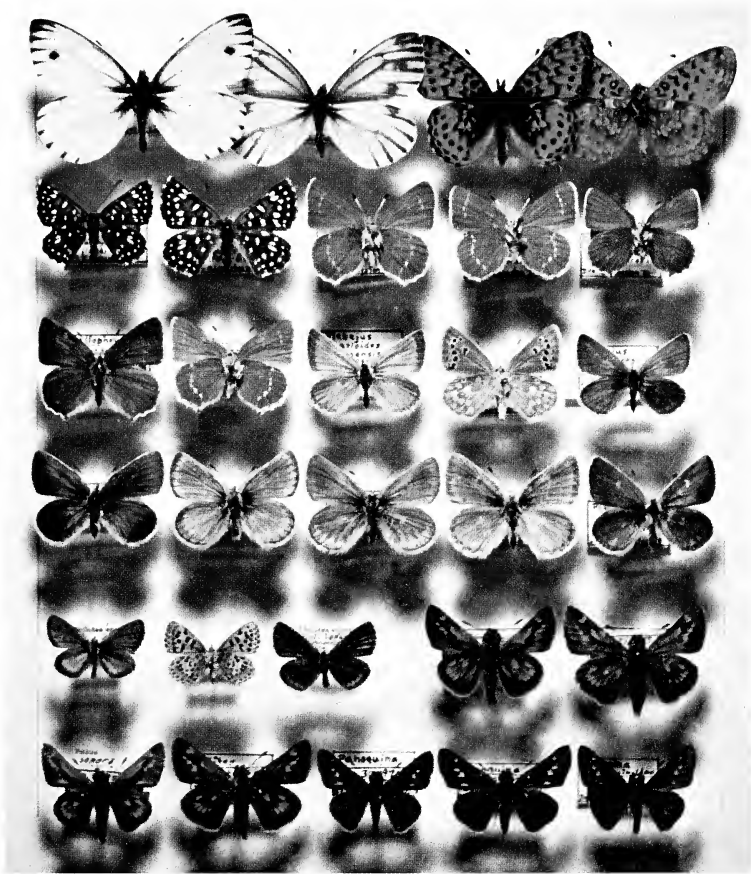


Fig. 4.—Examples from inland and high elevation populations. Localities in California, unless otherwise noted. All specimens leg. R. L. Langston.

Row 1.—*Pieris napi venosa*: 3 mi. NE. of Tuolumne City, Tuol. Co., ♂ 23 Mar. 1966; Rock Creek, 6 mi. NE. of Placerville, El Dorado Co., ♀ 12 April 1973. *Boloria epithore sierra*: Wet Meadow, 6900', above N. fork Stanislaus River, Tuolumne Co., ♂ 9 July 1969; Big Meadows, 6550', Hwy. 4, Calaveras Co., ♀ 30 June 1973.

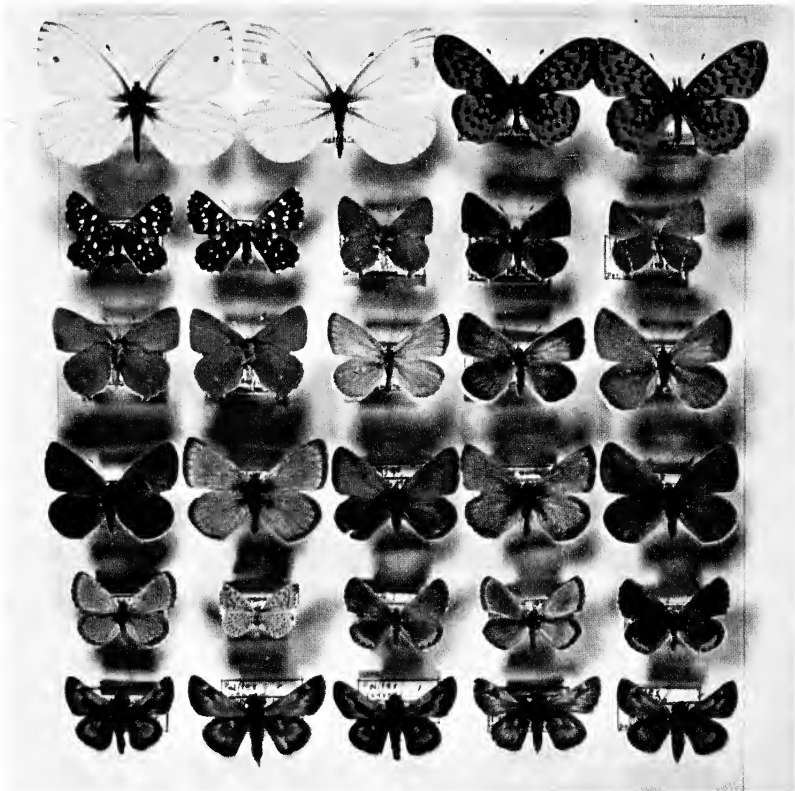
Row 2.—*Apodemia mormo mormo*: Del Puerto Canyon, Stanislaus Co., ♂ 21 Aug. 1962; ♀ 6 Sept. 1962. *Callophrys lemberti*: Upper Lyons Creek, 7800', El Dorado Co., ♂ 11 June 1972; ♀ 6 June 1970; SE. shore, Loon Lake, 6352', El Dorado Co., ♀ 9 June 1973.

Row 3.—*Callophrys dumetorum*: Dunes 1 mi. E. of Antioch, Contra Costa Co., ♂, ♀ 11 April 1954. *Plebejus icarioides ardea* (Edwards): Angel Lake, 8000', Elko Co., Nevada, ♂ 26 June 1972; 5 mi. SW. of Henefer, Summit Co., Utah, ♀ 27 June 1972. *P. i. lycea* (Edwards): Pole Mtn. area, 8640' Albany Co., Wyoming, ♀ 6 July 1972.

Row 4.—*Plebejus pardalis*: Hill SW. of Paradise Cay, Marin Co., ♀ 23 May 1964; Berkeley Hills, Alameda Co., ♂ 17 April 1954; ♀ 22 May 1954; Calistoga, Napa Co., ♂ 24 April 1956; Hill 3 mi. NE. of Vallejo, Solano Co., ♀ 11 June 1967.

Row 5.—*Philotes enoptes tildeni*: Del Puerto Canyon, Stanislaus Co., ♂ PARATYPE, 11 Aug. 1962; ♂ TOPOTYPE, 9 Sept. 1967; ♀ TOPOTYPE, 11 Sept. 1963; Polonio Pass, 3 mi. E. of Cholame, San Luis Obispo Co., ♂, ♀ 27 Aug. 1973.

Row 6.—*Polites sonora sonora*: E. shore, Bucks Lake, 5153', Plumas Co., ♂ 23 June 1949; King Canyon W. of Carson City, Nevada, ♀ 22 June 1970; SW. of Genoa, 5700', Douglas Co., Nevada, ♂ 20 July 1964; Mineral King, 7831', Tulare Co., ♀ 3 Sept. 1949; Tioga Pass, 9941', Mono Co., ♀ 8 Sept. 1955.



Apodemia mormo mormo (Felder & Felder)

Based on numerous records (Opler & Powell, 1961), *A mormo* in central and northern California is almost certainly univoltine, with adults in greatest abundance in late summer. This is opposed to *A. mormo virgulti* (Behr) which is multivoltine, with records from February to November. On this and other bases, it is felt by myself and others (correspondence, Mike Toliver), that *virgulti* may be a separate species.

On the sand dunes west of Seaside, Monterey Co., this "univoltine" *mormo* has been recorded from 4 July to 14 October in various seasons (Opler & Powell, 1961). Both sexes (with some worn) were taken on 4 July 1959, so the probable season started in late June. In several other seasons fresh and worn specimens were taken in August and September.

Further inland, at Del Puerto Canyon, western Stanislaus County, *mormo* were found only from mid-August to mid-September. This canyon in the Inner Coast Range was also visited several times in early August and no metal-marks were found.

Callophrys viridis (Edwards)

The upper ridges of the San Bruno Mountains, San Mateo County, are four miles inland from the coast. Although not on the immediate coast like the dunes, they certainly get their share of wind and cold, chilling fogs. Adults of *viridis* were recorded from the San Brunos from 26 Feb. 1963 to 4 June 1963 (Gorelick, 1971). This is definite for a single season, with numerous records for March and April in this and other years. The lower black bar represents slightly later dates for the populations on the dunes at Point Reyes, Marin County—30 March to 18 June (Gorelick, 1971). Since this is based on fewer records, the season probably extends from a little earlier to somewhat later.

After the data was compiled for the Gorelick study, *viridis* was discovered much further south—at the Marina Beach dunes, Monterey County by J. F. Emmel and the author on 11 May 1969. Large numbers were subsequently collected here in April and May, 1970-1973. All of these dates are well within the seasonal extremes of the northern populations.

Callophrys dumetorum (Boisduval) is found further inland in the dunes east of Antioch, Contra Costa County. The dates span from 18 March to 20 April (Gorelick, 1971; Opler & Lang-

ston, 1968). Throughout its extensive range most records are in March and April. The published records go from mid-February to early June, but not more than about a month at any single locality.

Callophrys lemberti Tilden is found much further inland and at higher elevations. Fewer records are available for this species. Its peak flight appears to be in early June at the 6 to 8000 foot levels in El Dorado County, and late June at 9 to 11,000 feet (Tioga Pass and Hoover Wilderness area, Mono County).

Plebejus icarioides moroensis (Sternitzky)

The dunes near Oso Flaco Lake, San Luis Obispo County have been visited by various collectors, but usually in different seasons. The earliest in the season appear to be 1 and 9 March 1972 by Bill Swisher, with *moroensis* recorded in April and May in other years. My latest record is 6 June 1966 when long series of mostly fresh ones were taken by myself and others. Therefore, the season probably extends at least another two weeks. It was not found on these dunes in August and September. The types were taken at Morro Beach, S.L.O. Co. on 27 June 1929. This is about 40 mi. NNW. of the populations indicated by the long black bar. J. A. Powell has also taken it sparingly in July on dunes to the north of Oso Flaco Lake. (These two are shown by the short black bar.)

The *icarioides* in the higher Sierra Nevada and the White Mountains, Mono County are dated from mid-June to mid-July. According to Downey (1962), "... members of a local population can be found in an area for about a 2-month period." Mid-June-July records are also prevalent for some of the other named subspecies in Nevada, Utah and Wyoming (specimens in Fig. 4).

Plebejus icarioides missionensis Hovanitz

The types were taken 1 April 1934 on Twin Peaks, San Francisco. Not far to the south, in the San Bruno Mountains, San Mateo County, I have taken it on 4 April 1971 and 27 June 1971—these extremes for a single season. There are numerous April, May and June dates in other years.

For comparison, *Plebejus pardalis pardalis* (Behr) was chosen from one colony in the Berkeley Hills—less than 20 miles to the northeast, but not on the immediate coast. The dates are 17 April 1954 to 22 May 1954—again a single season at the same place. This correlates with extensive records for *pardalis* in Contra

Costa County (Opler & Langston, 1968) from six distinct localities—all in April and May, none in March or June.

Plebejus pheres (Boisduval)

Originally described from San Francisco, it is now presumably extinct within the City—possibly its demise was similar to that of *Glaucopsyche xerces* (Boisduval). A morphologically close population to *pheres* is still found on the dunes at Point Reyes, Marin County. It has a flight period extending from mid-April to early July [2 July 1945, 1 ♀] based on examples at the California Academy of Sciences.

Further inland, *Plebejus pardalis* is again compared from the northeast—Napa and Solano Counties. The flight period appears to be late April to early June, with almost all of the records in May.

Philotes enoptes smithi Mattoni

On the dunes west of Seaside, Monterey County, this subspecies has been recorded from 20 June to 4 Sept. in various seasons. Most of the records are in August, but long series have been taken on several dates in July.

Further inland, *Philotes enoptes tildeni* Langston is found in the Inner Coast Range adjacent to the San Joaquin Valley, usually in August and September. The stippled bar represents one season at Del Puerto Canyon, western Stanislaus County. Only two fresh ♂♂ were taken 11 Aug. 1962, and the last collections were made 6 Sept. 1962. This is based on most of the type series cited in Langston (1963). In various other years the known dates go from 31 July to 11 Sept.

On 23 May 1967, six ♂♂ were taken in Del Puerto Canyon by Glenn Gorelick, and on 17 May 1973 another four ♂♂ by Jim Mori, indicating a spring flight (at least in some seasons). As with almost everything biological, there seem to be exceptions or “freak” occurrences.

Both *smithi* and *tildeni* could extend into late September or October, but I have no records of their actually being collected. This is predicted by correlation with *Apodemia mormo*, which is abundant at both localities and has the same *Eriogonum* hosts.

Polites sonora siris (Edwards)

West of Plantation in coastal Sonoma County, I collected good series of *siris* on 5 May 1955 and 23 July 1955—in the same season. It was present other years in June, early and mid-July. However, it was not found on visits to the exact same spot in

August and September. July specimens from western Washington are illustrated for comparison (Fig. 3). These show little variation from those in coastal northern California.

Polites sonora sonora (Scudder) is found in the Sierra Nevada at moderate to high elevations. More records are needed, but based on the few I have available, it flies from mid-June to late July from 5000 to 7000 feet, and in August to early September from 7000 to 10,000 feet.

Panoquina panoquinoides errans (Skinner)

This is the only other skipper in the whole Superfamily Hesperioidea that to my knowledge is restricted to the immediate coast of California. It violates the theme of those previously mentioned, as it probably has two or more generations per year. Comstock (1927) indicates it flying in mid-August and September. Most collections (especially those with large numbers), have *indeed* been in late summer. However, myself and others took it near Solana Beach, San Diego County as early as 19 June 1963, and it was still present on 1 July 1963—again in the same season.

Since there are no other species or subspecies of the genus *Panoquina* occurring in California, no inland comparison is made for *errans*.

DISCUSSION

Climate:

Outer Coast Range and *beach dunes* of California—mild winters and cool summers.

Very seldom does the weather go below freezing, or does frost occur on the immediate coast. On sunny days in January and February the south-facing slopes and the protected sides of the dunes can get quite hot. Since it does not get extremely cold at night, the development of Lepidoptera (and other insects) can commence quite early in many seasons.

Conversely, in the summer the coastal slopes and dunes are successively plagued by long periods of cold winds and fogs. In some places for several days in a row (or even weeks) the sun may not shine. During these periods, new individuals do not emerge from their pupae, and those already in the adult stage often remain quiescent. They do not carry on their activities of taking nectar, mating or ovipositing. When the weather becomes clear and sunny before the next siege of fog, the adults resume their activities.

Inner Coast Ranges and *Sierra Nevada* of California—cold winters and hot summers.

The insect season is shorter inland, particularly at the higher elevations. Below freezing and winter frosts are common in the Inner Coast Ranges. Heavy snows and several months of below freezing are characteristic of the Sierra Nevada.

In the spring, the days may warm up suddenly, even though the nights may still be below freezing. When the days have warmed, it generally stays warm and gets progressively hotter as summer approaches. This will instigate rather quick and near total emergence of adults in a short period of time. With nothing to delay them, the adults take nectar, mate and oviposit. With all activities completed, the flight period is soon finished.

Host plants:

Directly correlated with the climate is the condition of the larval food-plants. It is not the purpose of this paper to specifically record the hosts of the various Lepidoptera concerned. Therefore, I will treat only some of the examples, and for brevity refer to the hosts by genus only.

Pieris napi venosa in the Coast Ranges seems to prefer *Dentaria* (milk-maids), although Bruce Walsh (personal correspondence) of Carmel Valley has also found it ovipositing on *Arabis* (mustard). This could well be an alternate host for it and gen. aest. *castoria*. On the immediate coast the *Dentaria* stays in green succulent growth for a long time. Further inland it grows faster, blooms and dries out rather quickly. Possibly the populations of *venosa* inland do not work over to several other cruciferous plants that would appear "suitable." This could explain the absence of *castoria* and a shorter adult flight of *venosa* in the more inland areas. On the West Slopes of the Sierra Nevada, one of the hosts appears to be *Radicula* (water-cress) found in slow-moving parts of creeks and the seepage from springs.

Apodemia, coastal *Callophrys* and *Philotes* are well documented in the literature (Opler & Powell, 1961; Gorelick, 1971; Langston, 1969, respectively) as feeding on various species of *Eriogonum* (wild buckwheat). In the coastal areas the *Eriogonum* has considerable leaf growth early in the season. The flowers develop over an extended period from spring through summer.

By mid-summer the plants in a local area may be in various stages of bud, blossom or seed. Further inland, each separate species of *Eriogonum* tends to bloom "all-at-once," with the flowers soon becoming unattractive, even as a nectar source.

The *Plebejus* species cited are all recorded as having various species of *Lupinus* (lupine) as their larval hosts. According to Downey (1962) the peak adult flight period seems to occur at about the same time as seed formation in the host lupines. The eggs are deposited singly on leaves, stems, flowers and seed pods. On the coastal dunes the lupines (especially the large yellow-flowered perennial) remain green and succulent all year. The blooming period is very staggered, with buds, flowers and young seed pods at the same time on the same and/or adjacent plants. Further inland and at higher elevations, most lupines are in bloom for a relatively short time in the "spring," set pods, and soon become incompatible as hosts.

SUMMARY and CONCLUSIONS

Several species of univoltine Rhopalocera found along the coast of California have very long adult flight periods. This is due to mild winters and cool summers, combined with the resultant staggered development of the various larval food-plants.

Just a short distance inland in the Coast Ranges and further inland in the Sierra Nevada, these same species (or closest known taxa) have much shorter adult flights. This is due to cold winters, warming in spring and hot summers. These short flight periods are also correlated with increased elevation and a rather quick and uniform development of the larval food-plants, and their soon becoming unsuitable.

Examples of ten coastal entities among the families Pieridae, Nymphalidae, Riodinidae, Lycaenidae and Hesperidae are compared with their inland counterparts.

ACKNOWLEDGMENTS

Some of the examples in this study were taken from my field notes while on collecting trips with the California Insect Survey. I wish to thank Dr. J. A. Powell, University of California, Berkeley and others involved with the Survey for the opportunity to make these collections. Specimens were examined at the California Academy of Sciences, San Francisco for additional records. I am indebted to Dr. P. H. Arnaud for his cooperation and ac-

cess to the CAS collections. I am grateful to the many who have contributed to the Zone 1 Season Summary since I became coordinator. Data was gleaned from their contributions, and particularly the related correspondence of those mentioned in the text.

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APPENDIX

Many of the dates and locations cited in the text are based on specimens in the two accompanying photographs. These data are given in the legends to the figures.

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HABITAT: BREPHIDIUM PSEUDOFEA (LYCAENIDAE)¹

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Brephidium pseudofea (Morrison) typically is found in association with *Salicornia bigelovii* (Chenopodiaceae), the only definitely known host plant, along the coasts of Florida and somewhat further north. The illustration is of an area along the west coast of central Florida: Cedar Key, Levy County (19 Dec 1973).

Salicornia virginica is the predominant plant in the foreground, with some *Salicornia bigelovii* mixed in, left. Perhaps *S. virginica* is an alternate host; Rawson (1961, J. N. Y. Entomol. Soc. 69:88-91) has also suggested *Batis maritima*. *B. maritima* is a prostrate plant with succulent leaves growing near the *Salicornia*. The saltmarsh grasses to the left and in the background are mostly *Spartina alterniflora* (Gramineae). Bushes in the picture include *Avicennia germinans* (Verbenaceae) (large bush, right) and the smaller *Lycium carolinianum* (Solanaceae) (center, right), the latter in bloom and attracting other lepidopterous species (*Danaus*, *Agraulis*, *Urbanus*, *Panoquina*) but no *Brephidium* were observed on the *Lycium* flowers. *B. pseudofea* flies in colonies as many other lycaenids tend to do and has been reported to be generally uncommon in Florida, encountered in numbers only occasionally. Flight records are year round in the southernmost areas except for the months of August and November (Kimball, 1965, Lep. Fla., p. 49).

¹Florida Agricultural Experiment Station Journal Series No. 5309.

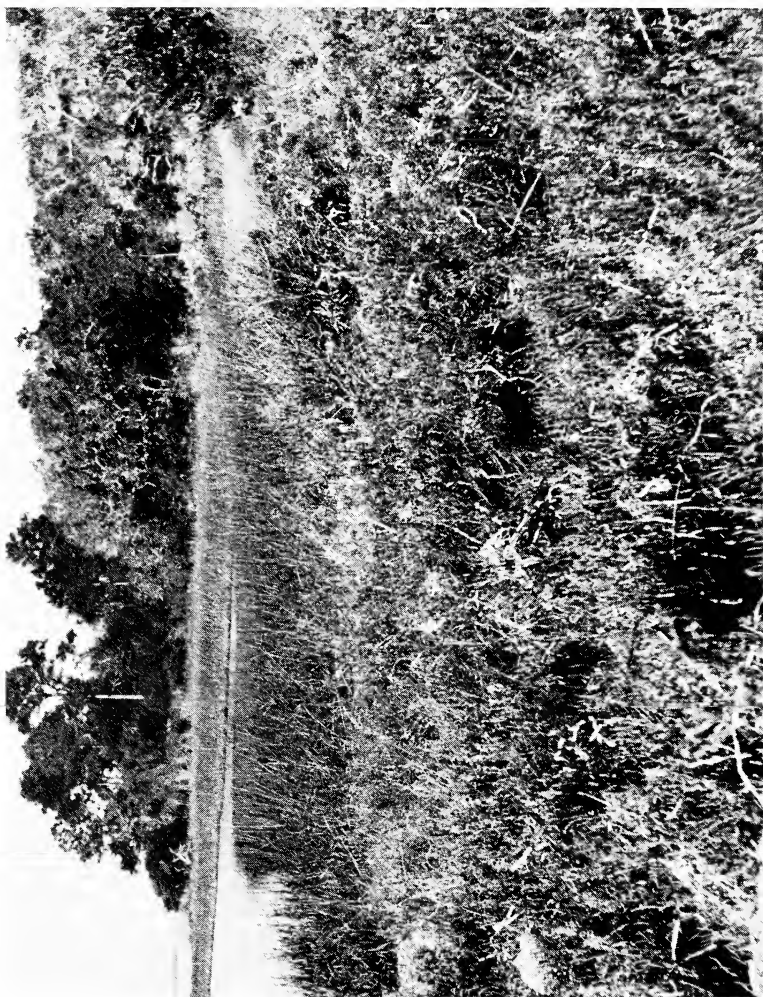


Fig. 1.—Coastal strand with *Salicornia* spp. in foreground on west end of Cedar Key, Levy Co., Florida. (19 Dec 1973)

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THE EARLY STAGES OF VARIOUS SPECIES OF THE GENUS *DIRPHIA* (SATURNIIDAE)

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INTRODUCTION

THIS PAPER IS ONE OF A SERIES describing the rearing in England of various Neotropical Saturniidae and deals with five species of *Dirphia*, as defined by Michener (1952). Eggs were sent to me by airmail; *D. avia* Stoll from Trinidad by Dr. A. D. Blest; *D. baroma* Schaus, *D. curitiba* Draudt, *D. lombardi* Bouvier, and *D. ursina* Walker, from St. Catarina, Brazil, by Sr. Fritz Plaumann. The first three of these were successfully reared through to adults, but the larvae of the last two died after several instars. The various stages were kept at 20-25°C., with occasional fluctuations of $\pm 5^{\circ}\text{C.}$ and under natural daylight conditions, but with additional light during the evenings while the stocks were being attended to. The duration of the various stages is summarized in Table 1.

DIRPHIA AVIA

From 375 eggs received 23.VI.61, a total of 205 healthy and 8 deformed pupae were obtained. In addition about 25 larvae were preserved.

The eggs—Laid in rather irregular batches. Shiny white with a small black micropyle. Virtually spherical 2.5 mm diameter. There is no prior indication before the larva hatches.

The larvae—In the 1st instar black with a dark brown head. Chalazae black, forked like a Y on the first 3 segments, simple, but a distinct bend two thirds of the way up, on the remainder. In the 2nd instar they become greyish dorsally, reddish-brown ventrally. In the 3rd instar the ground color a dirty white with black markings, these now persisting to the final stage, the ventral surface becoming less reddish and more like the dorsal as growth progresses.

The fullgrown larvae 8-10 cms long (the females being the larger). Ground color, including the head, a light grey with a tinge of green or violet, the color depending rather on how the larva is being viewed and the incident light. On each segment black markings, variable in both number and extent, the most prominent being a dorsal mark like a broad arrow () facing backwards and situated on each segment between the chalazae. The spiracles white, outlined in black. The chalazae grey; the spires grey with black tips; both have a violet sheen to them. The armature firm and fairly formidable. The thoracic chalazae and spines particularly long, overhanging and protecting the head. The prolegs with black crochets. The head grey with a broad inverted V above the brown mouthparts.

Larval habits—The larvae are gregarious throughout their life and wander about in long processionary columns. They feed by night and rest by day in a dense communal cluster. This was usually formed at the base of the foodplant which in this case consisted of a polythene water bottle containing the branches on which the larvae were being fed. So determined were the larvae to walk down the stalks that unless the neck of the bottle was extremely tightly plugged with Kleenex tissue, several of the larvae would drown themselves. When they are disturbed the larvae cling tight; they neither drop nor assume any unusual attitude, except that the head is slightly retracted and the thoracic spines lowered around it.

Sting—From the second to fourth instar the sting from the spines is about equivalent to that from a nettle (*Urtica dioica*), or a fullgrown *Automeris io* Fabricius. That of the fullgrown larva however is far more severe, as painful as that of wasps (*Vespa vulgaris* Linnaeus; *V. germanica* Fabricius), but shows only the usual type of Histamine reaction (Jones & Miller, 1954) bleb which soon wears off although the area is a little tender for a few days.

Pupation—This species was the first of the Neotropical Hemi-leucinae to be bred by the author and their unusual habits and individual idiosyncrasies were still strange to him. The finding of the correct foodplants and the optimum conditions for pupation were as yet unknown. The *D. avia* were therefore given a standard choice by being given a layer of peat overlain with moss in their rearing cage. This gives all the conditions required by species that pupate (a) in rolled leaves; (b) in litter; (c) underground. This species proved to be one of the few per cent

that is not satisfied with any of these three usual alternatives and demand specialized treatment.

When they are ready for pupation the larvae turn a purplish-red color which gradually darkens as they restlessly hunt for a suitable site over two or three nights. However, once the cocoon has been spun, the pre-pupa assumes the original larval color except for the spines, these remaining purple.

In their cages they wandered endlessly around, but during the day took their place in the communal resting cluster. Only about a dozen actually spun cocoons in the cages and over half of these failed to form normal pupae. Seeing that they were so obviously unhappy in the cages the larvae were removed and placed either singly in $\frac{1}{2}$ lb. tins or in pairs in 2 lb. tins. These tins contained a wad of sphagnum moss on top of a few inches of moist peat. They were fitted with tight metal lids and were used on the theory that the larvae were seeking somewhere totally dark. Be that as it may, all the larvae put into the tins pupated successfully. They formed a large flimsy papery cocoon between the peat and the moss, often attached to the side of the tin.

It is certain that in nature these larvae choose some specialized site; it is not unlikely that this is inside some species of Epiphyte.

Foodplants—The larvae were reasonably polyphytophagous on various temperate deciduous trees and one evergreen tree. The following were accepted: Hawthorn (*Crataegus oxyacanthae*); Beech (*Fagus sylvatica*); Plums, Cherries (*Prunus* spp.) Oaks (*Quercus* spp.—including *ilex*); Apple (*Malus* sp.). Black poplar (*Populus nigra*) and Privet (*Ligustrum ovalifolium*) were refused. Very freshly shooted Willow (*Salix* sp.) was eaten for the first two days by the newly hatched F1. larvae, but they so readily switched over to Evergreen oak (*Q. ilex*) that Willow was not considered really suitable. For the sake of convenience the larvae were mainly reared on Hawthorn and Beech, the F1 on Evergreen oak.

Adults—The majority of the pupae were disposed of and only a few kept for adult emergence. Two pairs were obtained, both of females that were three days old and had already laid a considerable number of eggs. Both these pairs were obtained when the temperature had been raised from 22°C to 30°C over some four hours and then dropped over one hour to 25°C. Several other moths placed together failed to pair. It is not

clear if the temperature fluctuation was of any significance or not. The two pairs occurred some five hours after sunset, the moths remained in copula for at least 90 minutes, had separated by morning.

From these two females a few small egg-batches were laid, in both cases laying only took place over about the 3 hours after dusk. About 75 per cent of the eggs hatched.

The adults lived for about 7 days. Females commenced to 'call' the same day as they emerged. Females started to lay infertile eggs in irregular masses if not paired after two or three nights, although even after this they would spend a short time calling each night. Males soon battered their wings to pieces after which they flapped rather helplessly on the cage floor.

DIRPHIA BAROMA

Eggs of this species were in a packet that arrived 29.VIII.63 after being a month in transit from Brazil. There had been some shaking up and these eggs were mixed with those of *D. curitiba*. They had just hatched on arrival. All five were reared.

Eggs—The remains of the eggshells were indistinguishable from those of *D. curitiba* (see below).

The larvae—In the 1st instar body dark reddish-brown. Head shiny black. Chalazae off-white, blackish towards tips. No records were kept of intermediate instars, but by the third the larva had assumed the general pattern of the final. The final instar larva 8 cms long. The head and anal segments black. Ground color, ventral and dorsal, black, with a brick-red incomplete band on each segment laterally and dorsally. Legs black with red spots. Chalazae and spines pale blue. The chalazae short, the spines arising starlike fairly long. Rather uniform and regular on each segment. This arrangement in fact resembles that of *Automeris memusae* Walker or *A. nyctimene* Latreille.

Larval habits—Since there were only five specimens the larvae were kept throughout in a plastic box. Apart from the fact that they kept bunched together and fed by night, the sample was too small to give any clear indication of habits.

Sting—This was not experienced.

Pupation—When ready to pupate the colors faded. The larvae were removed to tins with moss and peat. They pupated underground in the peat, forming a cocoon similar to that of a Sphingiid.

Foodplants—The newly hatched larvae were offered Beech, Hawthorn and Laburnum (*Laburnum anagyroides*) on which they commenced to feed, but after a week they transferred to Beech. The final instar finished their development on Evergreen oak. The following were refused: Privet; Plum; Elm (*Ulmus campestris*).

Adults—After nearly three months all the pupae produced adults within a week. Unfortunately all five were females.

DIRPHIA CURITIBA

Eggs of this species were received in 1962 and again in 1963. Those of the first year were reared with virtually no larval mortality, but from the second year there was a high larval mortality from what appeared to be granulosis virus disease. This disease caused the gradual and total loss of the F1. larvae. The information below is based on the first lot received 29.IX.62, which were a month in transit.

Eggs—Shaped like a slightly flattened ovoid, color white with a large black micropyle. Laid in regular groups of several dozen eggs, fastened strongly to the substratum with a clear cement. It was noticed that infertile eggs were encircled by a wide grey band on the upper half. No prior indication to larval hatch. Eggshells partly consumed by the newly hatched larvae.

The larvae—In the first instar brownish, including spines, head black. Second instar similar. In subsequent instars greenish-grey with black markings. The fullgrown larva 7.5 to 10.0 cms long (the females doubtless being the larger). Dorsally the ground color greenish-grey, or brownish, ventrally whitish-grey. The whole body covered with an intricate series of black markings which vary very considerably between larvae, in some coalescing to form large blotches which run continuously from one segment to the next. The spiracles are white, lightly outlined in black. The whole larva densely covered with spined chalazae. These particularly large and dense on the thoracic segments, and the anal, being here at least 1.5 cms long, projecting over the head and to the rear, as in *avia*.

Larval habits—Similar to *avia*.

Sting—Similar to that of *avia*.

Pupation—Also similar to *avia* and it was necessary to remove the larvae individually to tins. They also turn purple when ready for pupation. The cocoon appeared to be a little flimsier than that of *avia*.

Foodplants—Having been informed by Sr. Plaumann that they fed on Juglandaceae, especially Walnut (*Juglandia regia*) this was offered, together with Plum and Laburnum. They commenced to feed on the Walnut two days after hatching but by the fourth instar the supply failed. Oak and Peach (*Prunus persica*) were offered and accepted. Holly (*Ilex* sp.); Privet and Laurel (*P. lusitanica*) were refused. Their development was completed on Evergreen oak.

In the F1 generation the newly hatched larvae refused to start feeding on Walnut. This had been forced and it might well be the the very fresh soft leaf is unsuitable in some way. The parents had of course been given late fall leaves. These F1 larvae, with about 20 per cent loss, eventually started feeding on Oak, but after two weeks all the larvae accepted Beech and completed their development on this. The F3 generation was fed entirely on Evergreen oak.

The newly arrived larvae in 1963 were given a choice of Walnut and Beech. All preferred the Beech. The F1 generation of these was offered and fed on Hawthorn (other leaf being unavailable). As already stated however all these died of what appeared to be virus disease.

Adults—These behaved in much the same way as *avia*. Probably because rather more were available pairing proved relatively easy, without the temperature fluctuation which occurred before the *avia* pairing. Pairing took place some 2-3 hours after dusk and lasted 1-2 hours although two to three pairs were still coupled the following morning. Not all the pairings produced fertile eggs. Females either laying fully fertile, totally infertile, or mixed batches. The females that laid totally infertile batches behaved as if they were laying fertile eggs. That is, they laid in regular batches. Virgins, after several nights 'calling' would lay in a jumbled pile. It seems as if the correct laying reaction is initiated by the act of coupling, not fertilization. In the conditions of captivity 100-150 eggs per female were laid. This is by no means their full potential, on estimate, less than half. Only 1 pairing was obtained of the F2 generation. Two pairings were obtained from the F3 but no viable eggs were laid. By now of course the stock was brothers and sisters already one generation inbred, so this is perhaps not surprising.

DIRPHIA LOMBARDI

Eggs of this species were received 29.IX.62 and were just hatching on arrival after a month in transit. Sr. Plaumann gave Lauraceae? as possible food. All the larvae died by the end of the fourth instar.

Eggs—As received these were laid in a jumbled pile. The color white with a black micropyle. In shape, a slightly flattened ovoid, 1.75 mm x 1.5 mm x 2.0 mm high.

The larvae—In the first instar the dorsal surface rather blackish, a dirty white ventrally and laterally. Head black. After feeding and growing a little the larvae become overall whitish with black spines. In the 3rd instar a green lateral stripe has appeared, ground color now greyish-brown. The ultimate death of the larvae appeared to be due to granulosis virus disease.

Larval habits—Processionary and gregarious in the first three instars.

Sting—Not experienced.

Pupation—None were pupated.

Foodplants—The newly hatched larvae were offered a choice of Black locust (*Robinia pseudo-acacia*), Plum and Beech. They commenced to feed on Plum on which they were kept throughout their life. Evergreen oak, and Laburnum which were offered in the 3rd instar were refused.

DIRPHIA URSINA

Eggs of this species were received 29.IX.62 and again on 22.X.64. None of the larvae survived beyond the end of the fourth instar. The first batch apparently died of granulosis virus disease. The second batch almost certainly died due to the failure to find a suitable food for them; due to their rather late fall arrival the plum known to be suitable had already nearly fallen and the unsuccessful attempts to find a suitable alterantive led to starvation and resultant debility in the first instar. None survived beyond the second.

Eggs—As received these were laid in a jumbled pile. The color off-white with a black micropyle. Almost spherical and about 2.0 mm in diameter.

The larvae—The newly hatched larvae are purplish in color, including the spines and chalazae, with a black head. There was a steady mortality of the 50 or so larvae that commenced to feed. The three that reached the fourth instar had hardly changed in appearance from the first.

Larval habits—Processionary and gregarious in the first few instars.

Sting—Not experienced.

Pupation—None were pupated.

Foodplants—The newly hatched larvae were offered a choice of Black locust or Plum. The latter was accepted. Accompanying the second batch was a note from Sr. Plaumann that they fed on Wistaria (*Glyzine*). In late October in England the only Wistaria leaves available were in an advanced state of senescence; once picked they dried up overnight, even when kept in a high humidity. There were, not unexpectedly, refused by the larvae which again accepted Plum. Decent green leaves of this too, were hard to find. Laburnum, Everlasting pea (*Lathyrus latifolius*) and Laurel were offered but refused.

DISCUSSION

I have been informed (Blest, *in lit.*) and by others who have had tropical experience, that many Tropical Lepidoptera, including specifically *Dirphia* and *Automeris* species are extremely difficult to rear where they occur. Either they refuse to accept any available foodplant offered, or they prove to have been attacked by parasites, or die of virus diseases. Larvae collected wild in the forest have been known to refuse to accept the leaves of an apparently identical tree to that on which they were found. Also it is not very easy to collect foodplant from the canopy of a tropical forest.

When translated to a temperate zone, natural parasites, but not inheritable virus diseases are eliminated. So too of course, are the natural foodplants. Since in the majority of cases these are unknown, it becomes a question of trying one tree after another until one that is acceptable to the larvae is offered. Once they have commenced to feed, other leaf may be offered later, either because it is more readily available, or simply to find out what range of plants are acceptable. In the case of these *Dirphia* the larvae of three species proved to be reasonably polyphytophagous on temperate zone deciduous trees. The other two, *ursina* and *lombardi* only accepted one, Plum, but the larvae only having been available late in the year, other leaf, acceptable to the first three, was not available. It is perhaps significant, however, that Evergreen oak was refused. Without this the first three species could not have been reared. It would appear that *ursina* and *lombardi* have a different food range to *avia*, *baroma* and *curitiba*.

The larvae of *ursina* and *lombardi* having died in the early stages, it is difficult to make a comparison between them and the other three. Nevertheless their general appearance and the arrangement of the chalazae and spines were similar to those of *avia* and *curitiba* in similar instars. The odd one out is *baroma* which as already mentioned, has a structure similar to that of certain *Automeris* larvae. Its mode of pupation is also unusual being dissimilar to that of any other *Dirphia* moth known to me, but similar to that of *Eudyarina venata* Butler (Crotch, 1956).

Little appears to be known about the life-cycles, but I have not carried out an exhaustive search of the literature. This would be no easy matter, as much of the literature likely to carry information concerning *Dirphia* (i.e., local South American journals) is not very readily available. Before and during this investigation some two dozen enquiries were made of various institutions and colleagues in the Neotropical area. None was able to give me any information.

In the conditions of captivity there was a life-cycle, in the three species reared to adults, of six months and two generations a year could be obtained. It is difficult to obtain precise information on the occurrence and number of broods of many tropical species, but it does appear that these *Dirphia* are normally single-brooded. The related *D. jörgenseni* Schaus (Schreiter, 1943) is single-brooded in Northern Argentina and my supplier in Southern Brazil, Sr. Plaumann, tells me that *curitiba* and other species are single-brooded. This data quite clearly shows that these species therefore, have a facultative light-controlled diapause, but the exact determining conditions were not clearly defined by the present investigation.

According to Crotch (1956) *Dirphia* larvae are said to be long, cylindrical, with long slender single spines emerging directly from the body; at least one species is thought to have large lappets; a few species appear to spin cocoons not unlike *Saturnia pyri* Schiffmüller. None of these statements is true of the five species described in this paper. It is true that *Dirphioptis eumedide* Stoll has two small paired 'lappets' (Gardiner, 1966), but these are neither large, nor in the position assumed. This species was included in *Dirphia* by Draudt (1930).

The following larvae, of which I have traced a published description, bear a structural similarity to *avia* and *curitiba*. *Eudyarina venata* Butler (Burmeister, 1879, as *Dirphia consularis*

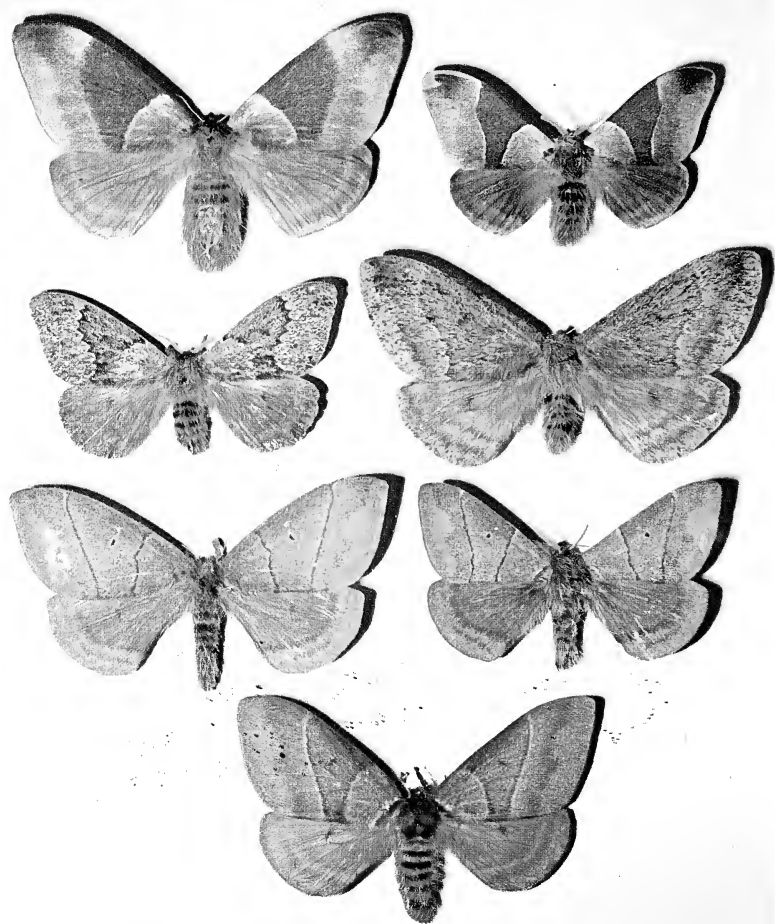


Fig. 1.—*Dirphia* imagines. Top, *avia*; second row, *curitiba*; third row, *ursina*; bottom, *baroma*, female only.

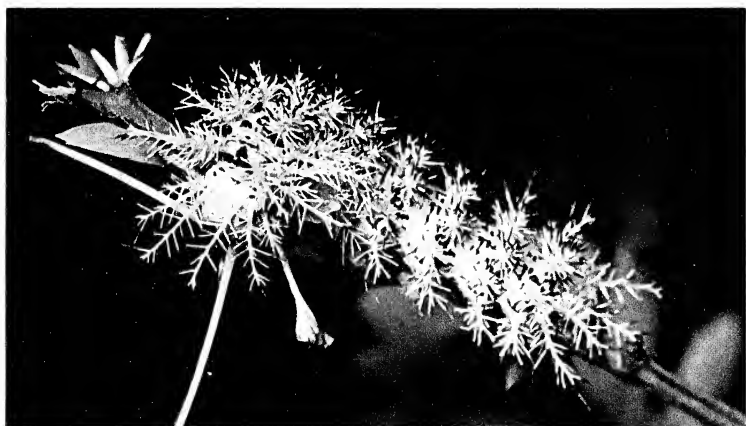


Fig. 2.—Larva of *Dirphia avia*.

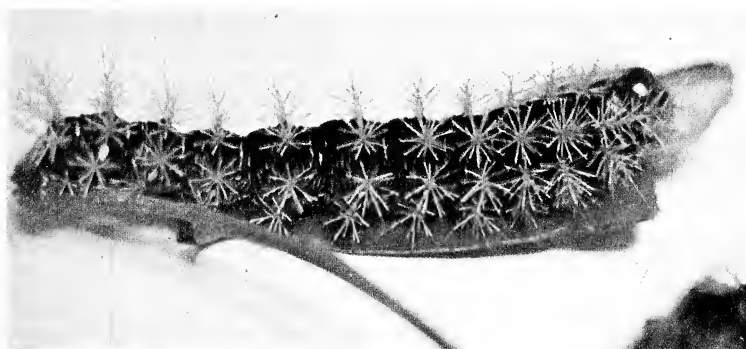


Fig. 3.—Larva of *Dirphia curitiba*.



Fig. 4.—Larva of *Dirphia lombardi*.

Burmeister); *Molippa sabina* Walker and *M. simillima* D.-Jones (D.-Jones, 1907). *D. jörgenseni* Schaus, however, (Schreiter, 1943) bears a remarkable resemblance to *baroma*, but pupates amongst the foodplant, not underground.

The question arises as to whether the present work on the larvae has any bearing on the confused issue of the classification of *Dirphia* and its relatives.

Draudt in Seitz (1930) divided the genus *Dirphia* into ten groups. This grouping was largely re-distributed by Michener (1952), some species being removed by him to separate genera, other genera of Draudt being brought into the *Dirphia* orbit. Although Michener uses a system of subgenera, I prefer, taking into account the larval characteristics and pupation habits, to regard his subgenera as separate genera. It is impossible from larval characters as at present known, to regard *Periphoba hircia* (see Gardiner, 1967) as being at all closely allied to for instance *Dirphiopsis eumedide* (see Gardiner, 1966) and *Dirphia baroma*, or the latter two to each other. *Dirphiopsis eumedide* shows similarities to *Dirphia jörgenseni* and they should perhaps be placed in the same genus but not *Dirphia*. On the other hand *E. venata* bears such a striking resemblance to *avia* or *curitiba* that it should be transferred back into *Dirphia*.

The larvae of *lombardi* and *ursina* at the time of their death in the fourth instar clearly resembled contemporary larvae of *avia* or *curitiba* and it is therefore considered that they too belong in *Dirphia*.

ACKNOWLEDGMENTS

This work was supported under a grant by the United States National Institutes of Health (Project GM-07109). Thanks are due to Dr. A. D. Blest for the photograph illustrating the larva of *baroma*.

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Fig. 5.—Larva of *Dirphia baroma*.

TABLE 1

The duration in days of the various stages in the life-cycle
of the *Dirphia* species

Species	Egg								Mean Total	Pupa
		1	2	3	4	5	6	7		
avia	30	8	8	7	4	4	8	25-37	70	62
baroma	34	9	10	7	12	10	13	0	61	82
curitiba	32	9	7	7	8	12	30-45	0	81	105
lombardi	31	7	7	10	-	-	-	-	-	-
ursina	31	6	11	11	-	-	-	-	-	-

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(Continued from page 82)

VOLTINISM AND HOST SPECIALIZATION

Opler and Buckett (1971), working with the large macro-moth fauna of Santa Clara County, California, suggest that the breadth of host specialization is correlated with voltinism; specifically, that univoltine species tend to be monophagous and multivoltines polyphagous. This correlation, if valid, suggests a primary biological basis for the adaptiveness of univoltinism: synchronization with a host plant which is seasonally limited in availability. Individual examples of such life cycles are well-known in North American butterflies. In some cases (e.g. *Pieris virginiensis* Edwards on *Dentaria*) the host plant is an ephemeral vernal species, annual or perennial. In others the edible part of the host is available only at certain seasons, even though the plant itself is present most or all of the year. This seems to be true of the insect faunas of tannin-rich plants. Tannins interfere with protein uptake, and the foliage of such plants is nutritionally useful only in spring before much tannin has accumulated (first demonstrated for the Geometrid *Operophtera* on oak by Feeny, 1970; probably applicable to *Satyrium*, *Erynnis*, etc.). Burns (1964) notes that the multivoltine *Erynnis tristis* oviposits and feeds on the young growth on evergreen oaks and avoids the older leaves. Such growth is limited in quantity and might be expected to be the object of intense competition among oak-feeding insects so long as the disadvantages of competition do not outweigh the advantages of rearing more than one brood a year.

Fair to good host plant data are at hand for 37 species of butterflies in the Sacramento Valley. These may be put into three categories of host specialization: monophagous, defined as restricted to a single plant genus in the geographical area in question; oligophagous, restricted to two or more genera in the same plant family; and polyphagous, feeding on two or more plant families. In the Valley all of the univoltine species are monophagous (Table 6), while just over two-thirds of the multivoltines are oligo- or polyphagous. Oligophagy is the commonest pattern: only three multivoltines (*Vanessa cardui*, *Plebeius acmon*, and *Papilio rutulus*) are polyphagous. Two of these are clearly colonizers. Most multivoltines have to change hosts during the season, but for many (*Pieris* on Crucifers, *Colias eurytheme* and *Everes comyntas* on Legumes) a seasonal succession of wild hosts of one family is available even in the absence of agriculture.

These data thus tend to bear out Opler and Buckett's suggestion. Univoltinism may result from other selection pressures besides host phenology, of course; perhaps it is better to say that both host specialization and voltinism are apt to be related to interspecific competition. Differences in phenology in different parts of the ranges of species may offer clues to selective factors acting on the timing of life history phenomena. *Lerodea eufala*, for example, is found only from June to early winter in both northern and southern California (Emmel and Emmel, 1973). Yet in the southeastern United States it flies all year, being recorded as early as ii.9 in coastal Georgia (Harris, 1972). *Brephidium exilis* flies nearly all year in southern California, but not before June in the Valley or at Suisun Bay; Opler and Langston (1968) record it as early as April in Contra Costa County, as does Tilden (1965a) for the San Francisco Bay area. In this case, however, it is not certain that *B. exilis* overwinters successfully inland at the latitude of Sacramento.

THE VALLEY AS A FAUNAL BARRIER

The Sacramento Valley is about 35 miles wide at the latitude of Davis. Across this expanse of flat land the habitats and plants of the foothills are absent, and many characteristic foothill butterflies (such as *Papilio eurymedon* Lucas, *Chlosyne palla* Boisduval, *Satyrium saepium* Boisduval, *Lycaena gorgon* Boisduval, *Callophrys dumetorum* Boisduval, *Thorybes pylades* Scudder) disappear as well. The data on the pristine vegetation of the Valley (Thompson, 1961) suggest that this barrier may have been much less dramatic in pre-American times. A few isolated pockets of foothill vegetation still exist in the Valley (e.g. Buckeye, *Aesculus californica* (Spach) Nutt., and Pipevine, *Aristolochia californica* Torr. on the north fork of Putah Creek near Barthel's Ranch, southeast of Davis). Along the intermittent streams such plants must have come down some distance below the mouths of the canyons, and they may have formed an element of the riparian forest on the permanent streams. Because of changes in the habitats, it is at present impossible to evaluate the historical role of the Valley as a barrier to dispersal between the Sierras and coast ranges. The butterfly faunas at comparable elevations are strongly similar across it, though at least three species (*Satyrium saepium*, *S. auretteum*, *Chlosyne palla*) are phenotypically distinguishable in the two ranges. At least one species, *Poanes melane*, was apparently continuously distributed across the Valley in riparian habitats but is now restricted to the two systems of foothills and the major riparian habitats

around Sacramento; it occurred at Davis (Willowbank?) as late as 1947 (Heppner, 1973). The present distribution of *Glauco-psyche lygdamus behrii* is very similar.

Eight or nine species of foothill butterflies enter the Valley more or less regularly but do not breed there. *Nymphalis californica* migrates regularly across the Valley floor (Shapiro, 1973); *Limenitis bredowii californica*, another strong flyer, is frequently seen at Davis. It is very unlikely that either of these species ever breeds in the Valley. In contrast, two relatively weak-flying Lycaenids, *Incisalia iroides* and *Lycaenopsis argiolus echo*, enter the Valley along the streams and have been recorded so often that both are suspected of breeding, although no known hosts are available.

A valid study of the effectiveness of the Valley as a barrier to faunal exchange must await a survey of the isolated Sutter Buttes in the mid-north Valley, planned for the next two seasons.

ENDEMISM AND EXTINCTION

The Willow Slough population of *Phyciodes campestris* is the most distinctive Valley endemic. Valley populations of *Everes comyntas* and *Limenitis lorquini* are phenotypically weakly distinguished, and *Satyrrium californica* has an unusual host (*Quercus lobata*). On the whole, however, the Valley fauna is strikingly lacking in endemic populations; it is composed largely of wide-ranging, vagile species with little tendency toward geographic variation.

It seems inevitable that more distinctive butterflies must have existed in the pristine Valley, with its well-developed plant communities of considerable antiquity. The Hesperidae in particular are lacking in the modern fauna; there is no Valley *Hesperia* of any kind, for example. It is conceivable that relict populations of undescribed Valley endemics may still exist in isolated or unexplored areas which have escaped intensive modification by man. The recent discovery of *Ochlodes yuma* in southern Sacramento County indicates that the list of Valley butterflies may not yet be complete. It is unlikely, however, that we will ever be able to reconstruct—or even guess intelligently—the composition of the pre-American Valley fauna.

FAUNAL LIST

Host plants are based on actual oviposition or larval records in the Sacramento Valley only. Botanical nomenclature is from

Munz (1970). Butterfly nomenclature is mostly as in Ehrlich and Ehrlich (1961) and skippers mostly as in dos Passos (1964). All records are for Yolo, Solano, and Sacramento Counties only. Flight periods for the 1972 and 1973 seasons are given in Tables 7 and 8 on a weekly basis.

Family Danaidae

1. *Danaus plexippus* Linnaeus. Monarch.

Common throughout. Four broods in both 1972 and 1973. Open country, especially along sloughs, ditches, and railroads with the host plants. No overwintering occurs in the Valley. The spring immigration from the west is more conspicuous than the autumn emigration. Tagged specimens recovered in the Valley and the Vacas indicate that at least some of our population overwinters in Marin County. *Host Plants: Asclepiadaceae; Asclepias fascicularis* Dcne.

Family Satyridae

2. *Coenonympha tullia californica* Westwood and Hewitson. California Ringlet.

Frequent but spotty, usually found in the Sacramento and American River floodplains, but not restricted to them. Throughout the season, as in the foothills; probably two broods, the second very protracted. Although breeding has not been confirmed in the Valley, this species is very probably resident. Generally absent from the heaviest clay soil areas.

Family Heliconiidae

3. *Agraulis vanillae* Linnaeus. Gulf Fritillary.

A rare stray. Since this species bred in the San Francisco Bay area in the 1960s it is perhaps capable of colonizing the Valley, at least temporarily. The normal hosts, Passifloraceae: *Passiflora* spp., are occasionally cultivated but there are no native species here.

Family Nymphalidae

4. *Speyeria callippe* Boisduval. Callippe Fritillary.

A rare stray; one male, fresh, v.9.72, northwest Davis. It is not known what subspecies or source area this individual represents. (Note: *Speyeria coronis* Behr has been taken at Suisun Bay (ix.23.72) and could stray into the Valley on the west side.)

5. *Euphydryas chalcedona* Doubleday and Hewitson. Common Checkerspot.

Occasional in floodplains, as at the American River and Putah Creek, probably as a stray from the foothills where it is abundant. No larvae have been collected in the Valley, where the usual host, Scrophulariaceae: *Diplacus*, does not occur.

6. *Chlosyne lacinia crocale* Edwards. Bordered Patch.

This species was not seen in 1972, but in 1973 about 15 were taken on the American River floodplain at Camp Pollock. These included all three color forms illustrated by Emmel and Emmel (1973). There were at least two broods. The Bordered Patch is indigenous to southeastern California, in the Imperial Valley and Colorado Desert, and seems to be unreported even as a stray anywhere north of the Transverse Ranges. Its future history in the Valley should be very interesting. *Host Plant*: The usual host, Compositae: *Helianthus annuus* L., is abundant on the floodplain.

7. *Phyciodes campestris* Behr. Field Crescent.

Very local. The Sacramento Valley populations differ from others seen in the smaller size and heavier infuscation dorsally (illustrated in Shapiro, 1974b). There is a large, vigorous colony along Willow Slough from northwest of Davis to the Yolo Bypass, and smaller colonies at north Woodland, Stone Lake-Beach Lake, and North Sacramento; strays to Davis, Willowbank, West Sacramento, mainly in autumn. Three broods. To be sought in

sandy bottomlands with good stands of the host. *Host Plant*: Compositae: *Aster chilensis* Nees. I took a female investigating *Aster novi-belgii* L., an eastern species, in a garden at Davis.

8. *Phyciodes mylitta* Edwards. Mylitta Crescent.

Common everywhere; four broods. Larva overwinters, feeding up in February-early March. *Host Plants*: Compositae: *Silybum marianum* (L.) Gaertn.; *Cirsium californicum* Gray; *C. vulgare* (Savi) Tenore; *Carduus pycnocephalus* L. *Centaurea solstitialis* L. is suspected.

9. *Polygonia satyrus* Edwards. Satyr Anglewing.

Uncommon, recorded mostly as singletons. Riparian forest (Southport, Sacramento River; Northgate, Sacramento State University area, both American River); once in Davis. Not confirmed to breed in the Valley, but the usual host, Urticaceae: *Urtica*, is common in the places where it has been found.

10. *Nymphalis californica* Boisduval. California Tortoiseshell.

Frequent as a transient in spring and fall, but not known to breed in the Valley where its usual hosts Rhamnaceae: *Ceanothus* do not occur. Completely absent during the hottest weather, and not appearing in spring until several weeks after it begins flying in numbers in the Vacas. In 1972 a significant west-to-east migration across the Valley occurred, beginning about v.26; in 1973 the same phenomenon occurred vi.8-11. The return, east-to-west movement was noticeable in Davis on x.1-x.3.73. (Note: *Nymphalis milberti* Latreille was taken at about 1000 feet in the Spenceville Recreation Area, Yuba Co., iv.11.73, and may reach the Valley floor on occasion northward.)

11. *Nymphalis antiopa* Linnaeus. Mourning Cloak.

Frequent to common in bottomlands and riparian forest; occasional elsewhere. Apparently one brood, becoming dormant by August and not flying again until February. Larvae colonial and often locally conspicuous. *Host Plants*: Salicaceae: *Salix lasiandra* Benth.; not seen on *S. hindsiana* Benth., the commonest willow in the Valley, but reportedly damaging *S. Babylonica* L. in gardens in Sacramento. The seeming avoidance of *S. hindsiana* may reflect its being widely utilized by larvae of the diurnal Saturniid *Pseudohazis eglanterina nuttalli* Strecker at the same time.

12. *Vanessa atalanta* Linnaeus. Red Admiral.

Common in the Sacramento-American River floodplains, and frequent throughout. Probably three broods. *Host Plants*: Urticaceae: *Urtica holosericea* Nutt., a common understory plant of riparian forest and thickets, absent in other habitats; also *Soleirolia* (*Helxine*) *soleirolii* (Baby's Tears), an introduced Urticaceous ground cover, in Davis.

13. *Vanessa* (*Cynthia*) *virginiensis* Drury. Painted Beauty.

Frequent in riparian forest, forest edges and nearby roadsides; rare elsewhere; the least common *Vanessa*, seldom seen before midsummer. Apparently four broods. *Host Plants*: Compositae: *Gnaphalium palustre* Nutt. (at Southport), probably other *Gnaphalium*.

14. *Vanessa* (*Cynthia*) *cardui* Linnaeus. Painted Lady.

Common and general. Immigrant, rearing three broods in 1972. 1973 was an outstanding year for this species, which flew for 44 weeks and bred in great numbers. Its migrations and variation are described in Shapiro (1974c). *Host Plants*: Extremely polyphagous, though in normal years mostly restricted to the plants marked *. Compositae: *Silybum marianum* (L.) Gaertn.*; *Cynara scolymus* L. (artichoke); *Carduus pycnocephalus* L.*; *Cirsium vulgare* (Savi) Tenore*; *Xanthium strumarium* L. var. *canadense* (Mill.) T. & G. (West Sacramento, v.26.73, larvae); *Centaurea solstitialis* L.; *Helianthus annuus* L. (Davis, vii.6.73, larvae common); *Wyethia glabra* Gray; Leguminosae: *Lupinus bicolor* Lindl. (oviposition near Winters, iii.18.72); Boraginaceae: *Amsinckia douglasiana* A. DC.*; Malvaceae: *Malva parviflora* L.*, *M. neglecta* Wallr.*; *M. nicaeensis* All.*; *Althaea rosea* L.; *Sida hederacea* (Dougl.) Torr. (larvae all season, Davis, 1973); Urticaceae: *Urtica urens* L. (Woodland Sinks, larva, v.13.73); Plantaginaceae:

Plantago lanceolata L. (Putah Creek, v.16.73, 3 larvae); Hydrophyllaceae: *Eriodictyon californicum* (H. & A.) Torr. (Putah Creek, vi.15.73; also seen in Amador Co.).

15. *Vanessa (Cynthia) annabella* Field. West Coast Lady.

Abundant, general, flying all year. Five to six broods. For figures and discussion of variation see Shapiro, 1974d. *Host Plants*: Malvaceae: *Malva parviflora* L., *neglecta* Wallr., and *nicaeensis* All.; *Althaea rosea* L.; *Sida hederacea* (Dougl.) Torr. (rarely).

16. *Precis coenia* Hubner. Buckeye.

Common to abundant in bottomlands and on sandy soils; frequent to common elsewhere. Restricted to bottomlands early in the season, but generally distributed by late vi. It is not certain that *P. coenia* overwinters in the Valley at all. It is abundant in foothill canyons (where it feeds on Scrophulariaceae, especially *Diplacus*) 3-6 weeks before it appears on the Valley floor. After late viii specimens, especially females, are very red or purplish beneath; but some clay-colored butterflies reappear after mid xi and until hard frost. The February butterflies in the canyons are clay-colored and undersized, and seem to be a mixture of fresh and worn individuals. *Host Plants*: Verbenaceae: *Lippia lanceolata* Michx. and (in cultivation) *L. nodiflora* Michx. vars. *canescens* (HBK.) Kuntze and *rosea* (D. Don) Munz; Plantaginaceae: *Plantago lanceolata* L. (at Vacaville, in lawns). Tilden's speculation (Tilden, 1971) that true *P. coenia* does not feed on *Lippia* is clearly in error; more than 100 wild larvae were collected from this plant at Davis and reared in 1973, and larvae have also been found on it at Fairfield.

17. *Limenitis lorquini* Boisduval. Lorquin's Admiral.

Common in riparian forest and among young willows along creeks, sloughs, and levees; very rare elsewhere, once seen on the University of California campus at Davis. Three broods. Valley specimens are, on the average, less orange and more bluish beneath than foothill ones. *Host Plant*: Salicaceae: *Salix lasiandra* Benth.; not seen on *S. hindsiana* Benth.

18. *Limenitis bredowii californica* Butier. California Sister.

Infrequent and sporadic. Not known to breed in the Valley, although acceptable oaks are locally available especially near the foothills. Probably formerly resident when the oak-Buckeye association extended farther down the streams.

Family Lycaenidae

19. *Atlides halesus* Hubner. Great Blue Hairstreak.

Common in riparian forest; frequent to common in residential neighborhoods with established deciduous trees; rare elsewhere. Three (perhaps a rudimentary fourth) broods. *Host Plant*: Lorantheae: *Phoradendron flavescens* (Pursh.) Nutt. var. *macrophyllum* Engelm., typically on Cottonwood along the rivers, on various other deciduous trees elsewhere.

20. *Strymon melinus pudica* Henry Edwards. Common Hairstreak.

Abundant throughout, breeding continuously; about five broods. A few specimens lack the postmedian line and shading on the forewing ventrally. One female with the orange completely replaced by white, Davis, vi.3.73. *Host Plants*: Malvaceae: *Malva nicaeensis* All. and *neglecta* Wallr.; *Sida hederacea* (Dougl.) Torr. (preferred). Euphorbiaceae: *Eremocarpus setigerus* (Hook.) Benth. suspected.

21. *Satyrium californica* Edwards. California Hairstreak.

Frequent and apparently breeding along the American and Sacramento Rivers, in relict stands of Valley Oak. Otherwise unrecorded except as strays along the edges of the Valley. Sacramento specimens are slightly smaller and darker than foothill ones. One brood. *Host Plant*: Fagaceae: *Quercus lobata* Nee. strongly suspected; no other likely host occurs in the river bottoms.

22. *Satyrium sylvinus* Boisduval. Willow Hairstreak.

Extremely abundant among young gray willows on floodplains and along sloughs and levees; less common in mature riparian forest; rare or absent

elsewhere. Variable in the spotting of the lower wing surfaces and in the extent of orange above. Apparently always fully tailed. *Host Plant*: Salicaceae: *Salix hindsiana* Benth., the common sandbar willow.

23. *Satyrium auretorum* Boisduval. Gold-Hunter's Hairstreak.

Six males and one female taken on the Sacramento River at Elkhorn Ferry, v.12.73 in mixed riparian forest on horehound flowers. These specimens are not phenotypically distinguishable from Vaca Mountains individuals.

24. *Incisalia iroides* Boisduval. Western Brown Elfin.

Occasional in riparian forest and as a stray down the creeks from the foothills. Not known to breed in the Valley, and none of the recorded hosts is present in spring in the riparian forest, but up to 6 have been taken in one day. (Note: The Bramble Hairstreak, *Callophrys dumetorum* Boisduval, is common in the foothills on both sides of the Valley but is unrecorded on the Valley floor although both Polygonaceae: *Eriogonum* and Leguminosae: *Lotus scoparius* (Nutt.) Ottley occur there.)

25. *Lycaena xanthoides* Boisduval. Great Copper.

Common to locally abundant along sloughs and ditches, in marshes and bottomlands, even in alkali marshes. Occasional on roadsides and in agricultural land. One brood in late spring. Females variable, with heavy to light spotting and much to little yellow flush above. *Host Plants*: Polygonaceae: *Rumex crispus* L., *R. conglomeratus* Murr., probably other *Rumex*.

26. *Lycaena helloides* Boisduval. Purplish Copper.

Abundant throughout: damp places, marshes, sloughs, ditches, alkali lands, dry waste ground with compacted clay soils, etc. Five broods, all season. Variable, especially the females; an albino female at Putah Creek, iv.17.72. *Host Plants*: Polygonaceae: *Polygonum aviculare* L. (dry places); *P. lapathifolium* L., *P. persicaria* L., *P. punctatum* Ell., *Rumex crispus* L. (all in wet places).

27. *Hemiargus isola* Reakirt. Reakirt's Blue.

Locally frequent to common, multiple brooded, waste ground near the American River. *Host Plants*: Leguminosae: *Melilotus alba* Desr.; *Medicago sativa* L.

28. *Leptotes marina* Reakirt. Marine Blue.

Locally common to abundant, multiple brooded, railroad and highway embankments and thickets near the American River, and occasional elsewhere. Perhaps not a permanent resident; much commoner in 1973 than 1972. *Host Plants*: Leguminosae: *Glycyrrhiza lepidota* Pursh.; perhaps also *Melilotus alba* Desr.

29. *Brephidium exilis* Boisduval. Western Pygmy Blue.

Extremely abundant on alkaline soils and in alkaline or saline marshes; common to abundant on waste ground with the hosts; occasional elsewhere. Probably does not overwinter in most or all of the Valley, but this needs to be confirmed. About four broods beginning in early summer, commonest after mid-August. *Host Plants*: Chenopodiaceae: *Atriplex hastata* (L.) Hall. & Clem.; *A. rosea* L.; *A. serenana* A. Nels.; *A. coronata* Wats.; *A. cordulata* Jeps.; *A. semibaccata* R. Br.; *Suaeda fruticosa* (L.) Forsk.; *Salsola kali* L. var. *tenuifolia* Tausch.; probably other Chenopods.

30. *Everes comyntas* Godart. Eastern Tailed Blue.

Common along ditches and sloughs and in bottomlands; occasional in moist waste ground and lawns. Five broods; the first with females strongly, the last with them more or less blue-tinted. The Sacramento Valley populations seem phenotypically distinct from others, so it is unlikely that they represent an introduction as has been suggested. *Host Plants*: Leguminosae: *Lotus purshianus* (Benth.) Clem. & Clem.; *Vicia villosa* Roth; *V. sativa* L.; *V. cracca* L.; *V. angustifolia* Reich.; *Lathyrus jepsonii* Greene ssp. *californicus* (Wats.) Hitchc.; *Trifolium tridentatum* Lindl.; *Lupinus nanus* Dougl. ssp. *latifolius* (Benth.) D. Dunn.

31. *Plebeius acmon* Westwood and Hewitson. Acmon Blue.

Common to locally abundant; waste ground, ditches, roadsides, levees,

creek bottoms; occasional everywhere. Five broods, the first of form *cottlei* Grinnell with blue females, the last with transitional males and largely black females. *Host Plants*: Leguminosae: *Lotus purshianus* (Benth.) Clem. & Clem.; *L. scoparius* (Nutt.) Ottley; *Melilotus alba* Desr.; Polygonaceae: *Polygonum aviculare* L.; *Eriogonum gracillimum* Wats. (sandbars, Broderrick).

32. *Plebeius icarioides* Boisduval. Boisduval's Blue.

A single, very worn male, West Sacramento, v.5.73, almost certainly a stray, but too battered to be determined to subspecies.

33. *Glaucopsyche lygdamus behrri* Edwards. Behr's Silvery Blue.

Locally abundant with *Lathyrus jepsonii* along the rivers; infrequent to common in creek bottoms and levee thickets throughout the Valley. Not seen elsewhere. *Host Plants*: *Lathyrus jepsonii* Greene ssp. *californicus* (Wats.) Hitchc. In the Vacas also recorded on *Vicia sativa* L., *V. villosa* Roth, and *Lupinus succulentus* Dougl., all of which also occur in the Valley.

34. *Lycaenopsis argiolus echo* Edwards. Echo Blue.

Infrequent in the American River bottomlands; entering the Valley elsewhere as a stray from the foothills. Breeding not established; the recorded host plants (Hippocastanaceae: *Aesculus*; Ericaceae: *Arctostaphylos*) are generally absent in the Valley.

Family Papilionidae

35. *Battus philenor* Linnaeus. Pipevine Swallowtail.

Frequent to locally common along the creeks near the host plant; occasional in mature riparian forest, and straying widely. One brood at Putah Creek, but perhaps partially four-brooded in Carmichael. *Host Plant*: Aristolochiaceae: *Aristolochia californica* Torr. Sometimes shows a "false brood" in very late fall or very early spring.

36. *Papilio zelicaon* Lucas. Anise Swallowtail.

Frequent to locally abundant on sandy floodplains as at Southport, West Sacramento, and at the American River; occasional throughout. *Host Plant*: Umbelliferae: *Foeniculum vulgare* Mill. Curiously unrecorded from other common Umbellifers, such as *Daucus pusillus* Michx.

37. *Papilio rutulus* Lucas. Western Tiger Swallowtail.

Common in riparian forest, orchards, and older city neighborhoods; occasional throughout. Three broods. *Host Plants*: Oleaceae: *Fraxinus* spp. (larvae, Davis); *Syringa vulgaris* L. (ova, Davis vii.27.73); Rosaceae: *Prunus caroliniana* Ait. (larva, Sacramento). Probably other trees (*Populus*? *Salix*? *Platanus*? other *Prunus*?)

38. *Papilio multicaudatus* Kirby. Two-tailed Swallowtail.

Frequent in riparian forest; apparently two-brooded. Host unrecorded; ash (Oleaceae: *Fraxinus latifolia* Benth.) or *Prunus* spp. (Rosaceae) suspected.

Family Pieridae

39. *Pieris rapae* Linnaeus. European Cabbage Butterfly.

Abundant everywhere; six broods, flying 42 weeks in 1972 and 49 weeks in 1973. The spring brood is heavily dusted beneath, with reduced dark markings above. A mosaic gynandromorph taken at Davis, iii.3.72, and another bred, iv.22.72. *Host Plants*: Cruciferae: *Brassica nigra* (L.) Koch.; *B. kaber* (DC.) Wheeler, *B. oleracea* L. cultivars., *B. geniculata* (Desf.) J. Ball.; *Cardaria draba* (L.) Desv.; *Sisymbrium officinale* (L.) Scop.; *S. irio* L.; *S. altissimum* L.; *Raphanus sativus* L.; *Lepidium latifolium* L.

40. *Pieris protodice* Boisduval and LeConte. Checkered White.

Common to locally abundant on sandy soils, especially on the American River floodplain; generally rare in clay areas, most widespread in viii-x. Not overwintering in most of the Valley, but colonizing widely in summer. Five or six broods, the first of form *vernalis* Edwards, the last transitional to it. The early spring brood is very local but may be common where it does occur. *Host Plants*: Cruciferae: *Brassica geniculata* (Desf.) J. Ball and *Lepidium latifolium* L. preferred; rarely on *Brassica nigra* (L.) Koch.,

(Continued on page 137)

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A NEW SPECIES OF *ORMISCODES*
(*DIRPHIELLA*) FROM MEXICO
(SATURNIIDAE: HEMILEUCINAE)

JULIAN P. DONAHUE¹ and CLAUDE LEMAIRE²

UNTIL NOW, the subgenus *Dirphiella* Michener contained only a single species. The second species, described here, differs remarkably in general appearance from *O. (D.) albofasciata*, although the two are structurally very similar. The females of both species are unknown.

Genus *ORMISCODES* Blanchard, 1852:61

Subgenus *DIRPHIELLA* Michener, 1949a:130 (nomen nudum!); 1949b:146. Type: *Dirphiopsis albofasciata* Johnson and Michener, 1948:11. Monobasic.

ORMISCODES (*DIRPHIELLA*) *TAYLORI* Donahue and
Lemaire, new species
(figures 1 and 2)

DIAGNOSIS

General appearance entirely different from that of *O. (D.) albofasciata* (figure 3), the only other member of this subgenus. *O. taylori* is easily distinguished from *albofasciata* by the yellowish brown ground color (dark brownish gray in *albofasciata*), completely yellow antennae (orange-yellow shaft and blackish rami in *albofasciata*), conspicuous, straight, double black and white postmedian band on forewing, from inner margin to apex (all white and sigmoid in *albofasciata*, from inner margin to costa), forewing apex acute (rounded in *albofasciata*), absence of color bands on dorsum of abdomen (present in *albofasciata*), presence of epiphysis (absent in *albofasciata*), and presence of apical cornutus on vesica of male genitalia (absent in *albofasciata*). In general appearance *taylori* is perhaps more reminiscent of members of *Dirphia* (subgenus *Dirphiopsis*) than of any other species of *Ormiscodes*.

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DESCRIPTION: Holotype male (fig. 2)

Head: *Antenna* pale yellow, scape clothed with small appressed scales, dark brown dorsally and paler ventrally; flagellum (37 segments) bipectinate to apex, rami with 2 or 3 terminal and subterminal bristles, the longest one 3 times as long as setae; ventral antennal cones conspicuous only on terminal 12 segments, increasing in prominence distally; each segment with 2-5 midventral setae, most numerous on distal segments, and 1 or 2 mid-dorsal setae on proximal 15 segments. *Eye* large, extending from antennal socket to ventral edge of frons, eye height three times shortest interocular distance. *Labial palpi* with blackish brown, appressed, hair-like scales which project ventrally. Vestiture of *frons* hair-like, blackish brown and erect dorsally, ventrally becoming almost black, projecting ventrad and curving slightly mesad. Vestiture of *vertex* consists of loose, spreading, grayish brown hair-like scales.

Thorax: Vestiture of loose, spreading, hair-like scales as follows: patagium anteriorly narrowly edged pink, centrally grayish brown, becoming darker laterally to blend with blackish brown of wing base; mesonotum with appressed brown hair-like scales, overlain by looser, paler scales. Mesoscutellum and metanotum with long, deep pink scales, extending posteriorly over first two abdominal segments. *Tegula* pale gray-brown. *Venter* of thorax densely clothed with hair-like scales, blackish brown between forecoxae and in anterior axillary region, deep pink elsewhere including a narrow longitudinal fringe parallel to and at the base of the posterior half of the hindwing. *Legs:* brown dorsally, paler ventrally and posteriorly, pink ventral fringe on femora and brown fringe on tibiae (posterior on foreleg, dorsal on mid- and hindlegs); *foreleg* femoral fringe pale pink, the hair-like scales paler at base; epiphysis large (nearly 1/2 tibial length), "J"-shaped, the apex projecting posterad, with pale yellowish white tuft internally and apically; first two tarsal segments with tapering dorso-posterior fringe; *midleg* as in foreleg but femoral fringe darker pink; external (ventral) surface of tibial spurs clothed with appressed pale brown scales; basitarsus with very weak dorsal fringe; *hindleg* identical to midleg except basitarsal fringe more strongly developed.

Abdomen: Dorsum of first segment clothed with long, loose, pink hair-like scales which overlay and conceal two narrow, transverse, subdorsal patches of short blackish brown scales on the posterior margin of the segment; dorsum of segments 2-7 uniformly clothed with small, spatulate, medium gray, appressed scales, intermixed with and almost totally concealed by much longer brownish black, semi-erect hair-like scales; dorsum of segment 8 and genitalia with tuft of loose, pink hair-like scales. Dorsal brownish black ground color extending ventrad to clothe pleural area, interrupted in the posterior fourth of each segment by a tuft of pink scales. Ventral vestiture of appressed hair-like scales yellowish brown, segments 2-7 with mesal grayish brown line.

Wings: General: ground color of both surfaces of wings yellowish brown, slightly paler on hindwing upperside; fringes paler; veins brownish black except across the white postmedial (PM) band on forewing upperside; discocellular spots absent on upperside, present on underside as narrow brownish black lines on R_{4+5} - M_1 crossvein of forewing and on anterior third of M_2 - M_3 crossvein of hindwing. *Forewing upperside:* antemedial (AM) line evanescent, a faint blackish shade arising at one fourth on inner margin, extending in nearly straight line, more or less parallel to outer margin, to the anterior margin of discal cell at a point approximately 1 mm proximal of origin of vein R_1 , then angling about 90° and continuing to the costa as a broader, more diffuse but darker shade, its course indicated by further darkening of veins where it crosses anterior edge of cell, vein Sc, and the costa; AM line bordered externally by a narrow, diffuse white shade, which expands abruptly at the anterior edge of the discal cell to

form an irregular, squarish, poorly defined whitish spot filling the area between the discal cell and costa, extending from the AM shade approximately to the origin of vein R_1 , the distal edge more or less perpendicular to costa. Area basad of the AM line is slightly darker between the costa and the posterior margin of the discal cell. Postmedial (PM) band conspicuous, oblique, blackish, about 1 mm wide, extending from inner margin at about three-fifths to apex at end of vein R_2 ; almost straight, but most notably offset outward in cell R_2-R_3 ; PM band bordered internally by a white band of similar width along its entire length, and bordered externally by a broad, obscure, fuscous shade, broadest at the inner margin, extending from tornus to vein R_3 , where it fuses with the PM band; outer margin of this shade dentate: concave on veins, convex in cells, the teeth strongest in cell Cu_1-Cu_2 and becoming weaker anteriorly. Costal margin dark brown from base to the white subcostal spot, concolorous with ground color beyond the spot. *Hindwing upperside*: postmedial band black, more or less parallel to outer margin, extending from inner margin at about three-fifths (where it widens on the margin itself) to the costa at seven-eighths, external edge diffuse, internally bordered by a narrower, diffuse whitish shade. Ground color basad of PM band slightly paler than area distad of PM band. *Underside* of both wings similar to upperside, except that the ground color of both wings is uniformly yellowish brown and the markings are less pronounced. *Forewing*: AM line and subcostal white spot absent, PM band weaker and more diffuse than on upperside, with internal white edging only faintly indicated and the distal shade absent; base of forewing with diffuse blackish shade corresponding to the weaker shade on upperside. *Hindwing*: compared to upperside, PM band slightly wider and more diffuse, internal white edge broader and more conspicuous; PM band weakly sigmoid, incurved between veins 2A and Cu_1 , excurved and more or less parallel to outer margin between Cu_1 and costa. Costa whitish from base to PM band. Subterminal band extremely faintly indicated, parallel to outer margin and slightly nearer it than to PM band.

Genitalia (fig. 3): almost identical to that of *Ormiscodes* (*Dirphiella*) *albofasciata* (as figured by Michener, 1952:488, figs. 328-332), with the conspicuous exception that the apex of the vesica bears a small, stout cornutus which that species lacks. In addition, the dorsal lobes of the valva appear to be slightly longer and basally broader in *taylori* than in *albofasciata*.

Size: forewing length 31mm.

Female: unknown.

Variation: the paratype differs from the holotype in minor details, as follows: smaller (forewing 28mm long); antennae with more flagellar segments (38 right, 39 left); proximal 20 (right) or 21 (left) segments with dorsal setae; markings and ground color of forewing upperside slightly darker: AM line more pronounced and the dentate shade distad of PM band much more conspicuous; underside of both wings darker: forewing with darker basal anterior shading, and the shade distad of PM band evident (as pronounced as on *upperside* of holotype); hindwing with subterminal band stronger, extending from vein 2A to vein R.

Additional material: excluded from the type series, but representing this or a very closely related species, is a slightly rubbed male in the LACM collection from 24 miles south of Valle Nacional, Oaxaca, Mexico, elevation 5,600 feet, 24-25 July 1970 (E. Fisher and P. Sullivan). This locality is approximately 120 air miles south-southeast of the type locality of *taylori*. The Oaxacan male bears a very close external resemblance to the type specimens, and may represent individual or geographic variation—a point that can be resolved only after the examination of additional material. This specimen differs from typical *taylori* as follows: slightly larger (forewing length 32.5mm), antenna with 42 segments, only the basal 10 with

single dorsal setae. Discocellular scaling conspicuous on upperside of both wings, and more pronounced on underside than in *taylori*. *Forewing upper-side* with AM line placed farther distad, entering discal cell at vein Cu₂ then angling across to origin of vein R₁ where it angles proximad to costa; white external edge of AM line broader, more conspicuous and more extensive, extending to vein 2A, almost completely filling the triangular portion of discal cell distad of AM line, and expanding to form the whitish costal spot farther distad than in *taylori*, the spot extending from origin of vein R₁ halfway to fork of R₂ and R₃; PM band directed to a point on costa *before* apex, then angling on vein M₁ and continuing, more or less straight, to a point just *below* apex. *Forewing underside* lacking fuscous suffusion in discal cell, PM band as above except angled at vein R₄ s. Fronto-clypeal protuberance produced into a truncate, triangular projection. There are also several slight differences in the shape of the uncus, gnathos, transtilla, and lobes of the valva of the male genitalia.

TYPES: HOLOTYPE ♂, 1 mile south of Pueblo Calcahualco, 8 road miles west of Coscomatepec, Veracruz, MEXICO; elevation 6,200 feet, 26 July 1972 (Terry W. Taylor); collected in the rain at a 15-watt fluorescent black light, between 10:00 and 10:30 p.m. Central Daylight Time, ambient temperature 45°F. (C. Lemaire genitalic preparation no. 2637, in glycerine).

PARATYPE, 1 ♂, same locality as holotype, 21 July 1973 (Terry W. Taylor and Roy R. Snelling); collected at a mercury vapor light between 10:00 and 11:00 p.m. Central Daylight Time, ambient temperature 59°F. Holotype and paratype deposited in the Natural History Museum of Los Angeles County, through the courtesy of Terry W. Taylor.

DISCUSSION

Michener erected the subgenus *Dirphiella* for the lone species *Dirphiopsis albofasciata* Johnson & Michener, then known from a single male from Chiapas, Mexico ("... presumed to be from the vicinity of Comitán."). It is unique among the nine subgenera of *Ormiscodes* in that the male antenna is bipectinate instead of quadripectinate. Michener (1952:445-446) later expanded the definition of this subgenus in his revision of the higher categories of the New World Saturniidae.

One of us (JPD) has examined the type specimen of *D. albofasciata*, and found that the original description is defective with respect to several antennal characters, as follows: the antennal shaft and extreme bases of the rami are orange-yellow, contrasting sharply with the brownish black of the rami (not "antennal shafts brown, rami black"); each antennal segment has two

stout, subapical, para-medial setae on the ventral side, plus numerous scattered, small, brown lateral setae which contrast with the color of the shaft; mid-dorsal setae not evident (not "segments of antennal shaft of male without setae or with a single dorsal subapical seta"); terminal bristle of rami about three times as long as longest setae, subterminal bristle present on some rami (not "terminal bristles of rami nearly twice as long as setae"). There are 39 segments in each antennal shaft. Unfortunately, it was not possible to verify the absence of the epiphysis, as the forelegs are represented by a single femur, and a patch of scales on the locality label, where one foreleg had apparently been glued and subsequently fallen off.

However, the junior author has verified the absence of the epiphysis in several specimens of *albofasciata* (all males) in his collection from several localities in Chiapas. These specimens indicate that *albofasciata* is very variable in color and maculation. The ground color of the upper surface of the wings varies from pale to deep black; the postmedian bands (sometimes partly or even entirely absent) vary in color from pure white to orange yellow; in specimens with the orange-yellow bands the median area of the forewing and the postmedian (and sometimes the median) area of the hindwing are more or less suffused with the same orange-yellow color or with yellowish brown; the width of the fringes varies, as does their white or yellow color, and there are generally black dots in the fringe at the ends of the veins.

With the discovery of this second species of *Dirphiella* it is necessary to modify the definition of the subgenus, as some of the original characters, as amended above, now appear to be of only specific significance. These characters as they occur in *taylori*, and their corresponding state in *albofasciata*, are as follows: epiphysis present in male (absent in *albofasciata*); antennal cones conspicuous only on terminal 12 or fewer segments (recognizable nearly to base in *albofasciata*); eyes large, height of eye three times shortest distance between eyes (subequal in *albofasciata*).

These differences, plus the entirely different facies, would appear to be sufficient to warrant the erection of a new subgenus for *taylori* were it not for the extreme similarity in genitalia.

We take pleasure in naming this species in honor of Terry W. Taylor, who collected the type series and brought them to our attention. We are further indebted to Charles L. Hogue

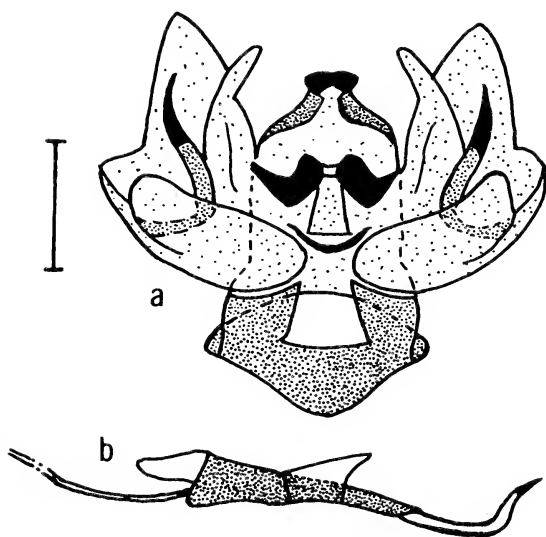


Fig. 1.—*Ormiscores (Dirphiella) taylori*, genitalia of male holotype: a.—ventral view, aedeagus removed; b.—aedeagus, lateral view.

for his valuable comments and suggestions on the manuscript, and to Frederick H. Rindge of the American Museum of Natural History, who kindly loaned the type specimen of *Dirphiopsis albofasciata*.

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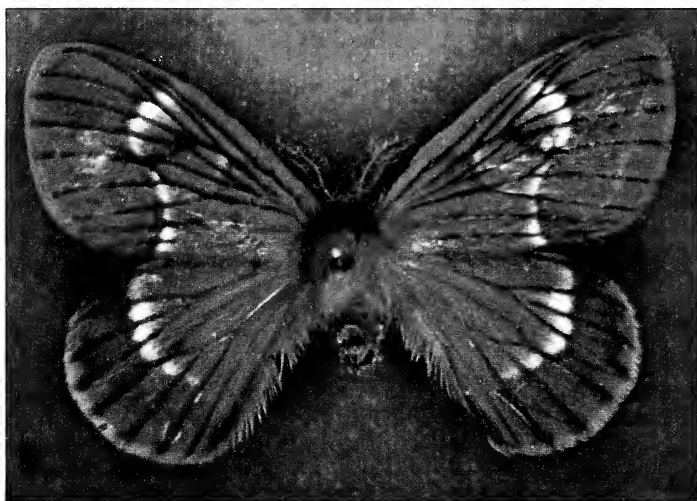
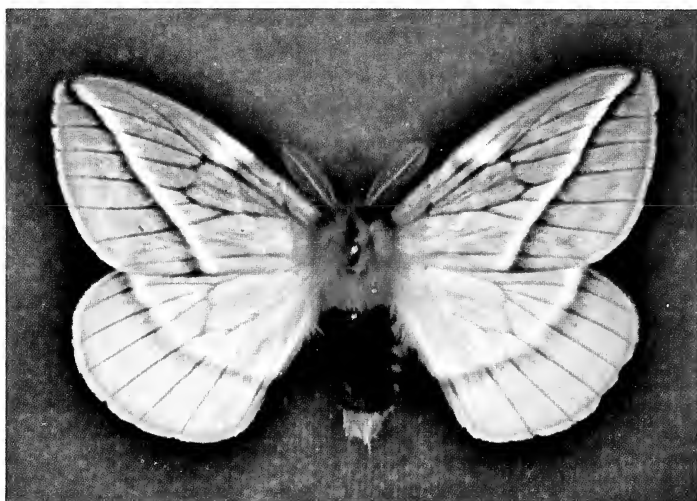


Fig. 2 (top).—*Ormiskodes (Dirphiella) taylori*, dorsal view of holotype male. Approximately 1.4 times actual size.

Fig. 3 (bottom).—*Ormiskodes (Dirphiella) albofasciata*, dorsal view of holotype male. Approximately 1.6 times actual size.

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A NEW SUBSPECIES OF
EUPHYDRYAS EDITHA FROM THE
CHANNEL ISLANDS OF CALIFORNIA

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IN OUR RECENT BOOK, *The Butterflies of Southern California* (Emmel & Emmel, 1973b: p. 34), we mentioned the occurrence of an unrecognized dark race of *Euphydryas editha* (Boisduval) on the Channel Islands off the coast of Santa Barbara and Ventura Counties, California. The purpose of this present paper is to formally describe this new subspecies. Publications already out (e.g., Emmel, 1967; Singer, 1971, 1972) and in preparation analyze the ecological, host plant, and evolutionary affinities of the various geographic sets of populations of *Euphydryas editha* in California and the other western states. These data will allow evolutionarily interesting comparisons to be made with information from similar studies in the *Euphydryas chalcedona* complex (Hovanitz, 1941, 1942; LeGare & Hovanitz, 1951; Emmel & Emmel, 1973a; Emmel, T. C., in preparation).

Euphydryas editha insularis, new subspecies
(Figure 1: a, b, and c)

Diagnosis: This is a very dusky, *blackish* subspecies with melanic scaling greatly reducing the moderate to extensive yellow and red spotting present on other coastal and montane *Euphydryas editha* subspecies in California. The type series specimens of five males and one female are slightly larger by one to three millimeters of forewing length than the average *E. e. bayensis* specimen from coastal central California (Emmel, 1967: p. 75-76). The two sexes are remarkably similar in wing coloration and pattern.

The forewings above have a faint, nearly marginal row of dull red spots and a faint submarginal row of small crescent-shaped cream spots. A wide black submarginal band bears a row of small

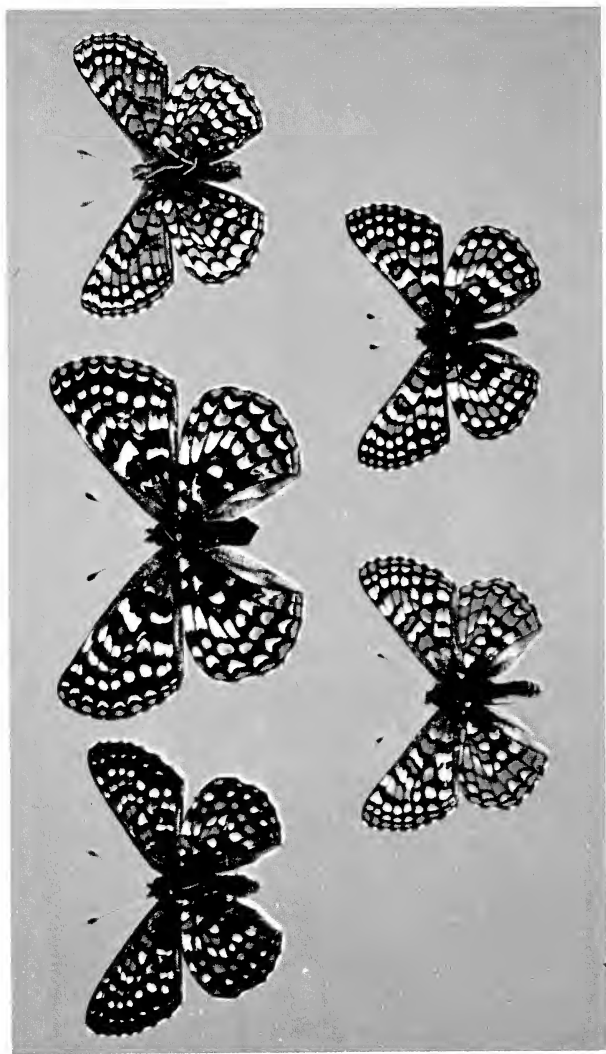


Fig. 1. — *Euphydryas editha* specimens from the Channel Islands and coastal California populations. Top row: (a) *Euphydryas editha insularis*, Emmel & Emmel, holotype male of new subspecies, Santa Rosa Island; (b) *E. e. insularis*, allotype female, same locality; (c) *E. e. insularis*, paratype male, ventral surface, same locality. Bottom row: (d) *E. e. nr. bayensis* Sternitzky, male, from population nr. Hwy. 198, 19 mi. E by S. from King City, Monterey Co., California, 17 April 1964, T. C. Emmel, leg.

cream spots. A nearly continuous row of cream-red spots follows in a median position, with one or two red spots alternating with cream spots extending posteriorly from the coastal margin of the forewing as one progresses basally from the median row. One cream spot is found posteriorly in the otherwise-black basal half of the wing.

The hindwings above exhibit five well-isolated rows of red and cream spots, alternately placed distally to proximally in a rich black ground color. There is a faint, nearly marginal row of small, dull red spots, and a submarginal row of slightly larger cream spots. There is a postmedian row of crisply-bordered, entirely dull red spots, of small size compared to mainland coastal populations (see Fig. 1). There is a median row of distinct cream spots (the spots in this row merge and become an essentially continuous band in *E. e. bayensis*, separated only by black-pigmented veins). Basal to this is a very faintly marked row of reddish spots, with the bottom half usually heavily melanic. Proximal to the body are several irregularly-shaped cream spots.

Ventrally, the forewing and hindwing patterns are strongly marked with red and cream with reduction of melanic portions to along wing veins *except* in the submarginal black band area on the forewing and in the postmedian area to the outside of the median row of cream spots on the hindwing. Only in these two areas do the underside pattern and coloration diverge notably from those of mainland populations by being blackish in aspect.

The subspecies is named for the type locality, the Channel Islands group off the coast of California. The type specimens were collected by Chris Henne in 1941 on Santa Rosa Island (one fresh female on March 31, and five fresh males on April 1). Henne (personal communication) describes the exact locality of the colony as being at the top of a rolling hill at perhaps 300 feet elevation, directly behind the ranch house on the Vails' Ranch. Poor weather prevailed during his visit (made with Lloyd Martin of the L.A.C.M.). One very worn *E. chalconota* male was taken on Santa Cruz Island, March 27, 1941, by Lloyd M. Martin; the specimen is labeled with the L.A.C.M. Channel Islands Biological Survey label (No. 1941-4707), and was placed in the Museum Collection with the series of six *E. editha* from Santa Rosa Island. However, it is clearly *chalconota*.

HOLOTYPE Male: Radius of forewing, 22.1 mm.; CALIFORNIA, Santa Barbara County, Santa Rosa Island, April 1, 1941. Collected by C. Henne. Los Angeles Museum Channel Islands Biological Survey. No. 1941-4831.

ALLOTYPE Female: Radius of forewing, 28.5 mm.; CALIFORNIA, Santa Barbara County, Santa Rosa Island, March 31,

1941. Collected by C. Henne. Los Angeles Museum Channel Islands Biological Survey. No. 1941-4755.

PARATYPES: 4 males, same locality, collector and survey number data as holotype.

The holotype, allotype, and paratypes are deposited in the collection of the Natural History Museum of Los Angeles County.

It is worthy of note that despite extensive correspondence with many California lepidopterists during the preparation of our book, no additional records or specimens of *Euphydryas* from the Channel Islands have come to light. The above seven butterflies were taken during the Los Angeles County Museum's Channel Islands Biological Survey (1941). Robert Langston of the University of California Medical Center at San Francisco has done subsequent field work on Santa Cruz Island and did not find *E. editha* in April; however, *Euphydryas chalcedona* (Doubleday) was found during a visit to this island by Langston from April 25 to May 1, 1966. None of the many lepidopterists who have collected on Santa Catalina Island in all months throughout the years has found *E. editha*. For that matter, *E. chalcedona* itself surprisingly has not been recorded from Santa Catalina Island (Meadows, 1936; Emmel & Emmel, 1973b).

A glance at the map of the relative positions of the Channel Islands in Figure 2 shows that the northern cluster of the four islands of Anacapa, Santa Cruz, Santa Rosa, and San Miguel is more susceptible to colonization from the few known coastal *E. editha* colonies (Emmel & Emmel, 1973) on the mainland, than are the relatively well isolated southern islands of Santa Catalina, San Clemente, San Nicholas, and Santa Barbara, particularly by a non-migratory and indeed relatively sedentary species (Ehrlich, 1965; Singer, 1972).

Historically, there is even stronger reason to see why *E. editha* would be found in the northern and not the southern Channel Islands. Thorne (1969) states that the northern group had terrestrial connection with the mainland down to perhaps a half million years ago, and that all these islands were interconnected with each other (but not with the mainland) during the Iowan or lower Wisconsin glacial stages from about 11,000 to 20,000 years ago, when sea levels were lower. There seems to be no evidence for the possibility of recent overland migration to the southern Channel Islands, due to their prolonged and complete submergence during the Pliocene and Pleistocene epochs (Thorne, 1969).

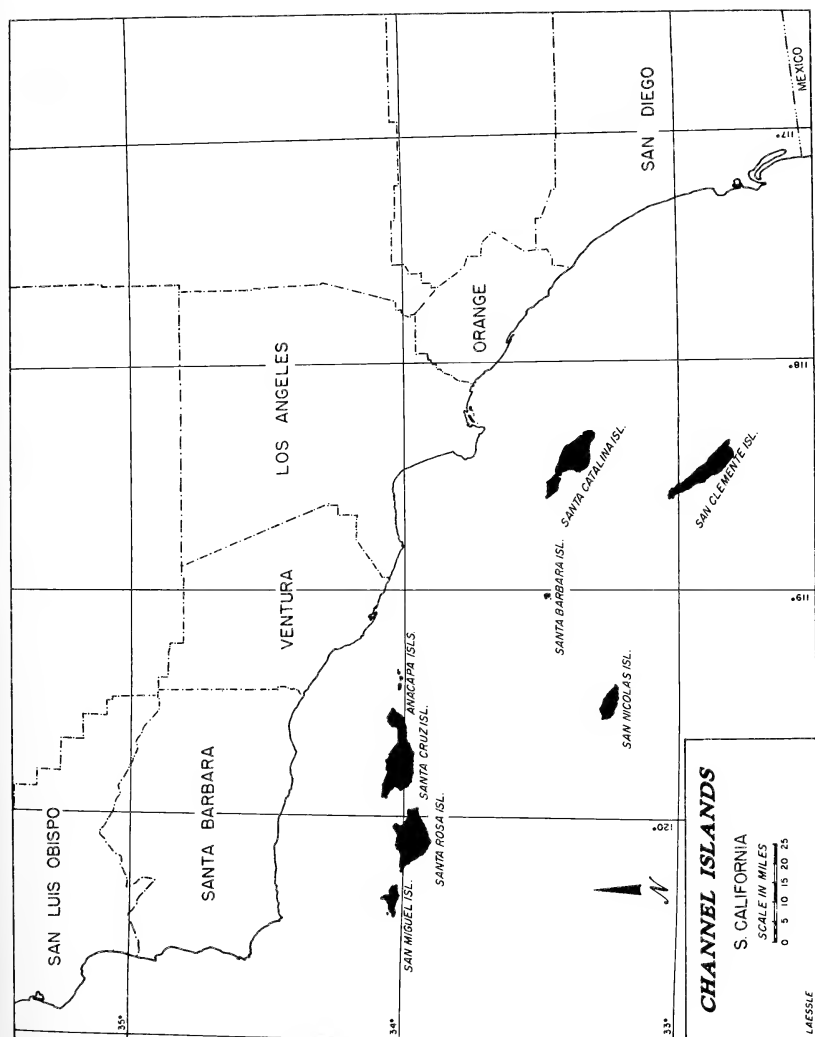


Fig. 2. — Map of the Channel Islands and the coastal counties of southern California.

One man-influenced factor contributing to the few records of butterflies from the northern Channel Islands in the past has been their private or Navy ownership and relatively restrictive policies on visitation. The establishment of several university laboratories on the isthmus of Santa Catalina and on Santa Cruz Islands, as well as Channel Islands National Monument on Santa Barbara, San Miguel, and Anacapa Islands, has made these sites easier to visit. Details of how to secure permission to visit these areas and the other islands are given by Thorne (1969: pp. 406-407). It is also worth noting that the native vegetation of several islands has been devastated by feral animals such as goats, and these islands may presently have no suitable habitats for *Euphydryas* colonies.

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(Continued from page 122)

B. kaber (DC.) Wheeler, *Raphanus sativus* L., and probably others.41. *Pieris sisymbrii* Boisduval. California White.

One male, American River, iii.14.73, presumably a stray from the Sierra foothills.

42. *Euchloe ausonides* Boisduval. Large Marble.Common on floodplains, along sloughs and ditches, straying elsewhere. Sacramento Valley specimens average much larger than those from the foothills, at least in late spring; most of the females are orange-tinted (*semi-flava* Comstock, *flavidalis* Comstock). In 1972 seemingly one-brooded with a very long emergence, but in 1973 clearly double-brooded with two temporal phenotypes. Males patrol territories along gullies or ditches. *Host Plants*: Cruciferae: *Raphanus sativus* L. (preferred); *Brassica nigra* (L.) Koch.; *B. napus* L. According to R. Langston, this species flies much later into summer in the San Francisco Bay area, but is still presumably two-brooded.43. *Anthocaris sara* Lucas. Sara Orange-Tip.Frequent in riparian forest along the Sacramento and American Rivers; occasional elsewhere along fencerows, ditches, etc. The second brood appears to be rudimentary. *Host Plants*: Cruciferae: *Brassica napus* L.; *B. geniculata* (Desf.) J. Ball; *Raphanus sativus* L.44. *Colias eurytheme* Boisduval. Orange Sulphur.Abundant throughout, especially in alfalfa fields, reaching greatest densities in ix. Six broods, the first and last of form *ariadne*, heavily shaded and with reduced borders and orange color above. Extremely variable, producing cream-yellow, pale green, buff and other unusual females mainly in autumn; a cream-white male, Davis, ix.10.72; chrome yellow females, Willowbank, viii.13.72, Willow Slough, ix.27.72 and x.26.72; yellow male, Willow Slough, ix.27.72. Flew 44 weeks in 1972 and 44 in 1973. *Host Plants*: Leguminosae: *Medicago sativa* L.; *Vicia angustifolia* Reich.; *V. sativa* L.; *V. cracca* L.; *V. villosa* Roth; *Lotus strigosus* (Nutt.) Greene; *Glycyrrhiza lepidota* Pursh; *Lathyrus jepsonii* Green ssp. *californicus* (Wats.) Hitchc.45. *Colias* (*Zerene*) *eurydice* Boisduval. California Dog-face.Rare stray in the Valley (Davis, iv.26.72, vi.7.72). Not known to breed, although the usual host, Leguminosae: *Amorpha californica* Nutt., grows at Elkhorn Ferry.

Family Hesperidae

46. *Epargyreus clarus* Cramer. Silver-Spotted Skipper.Infrequent, mostly near the host plant (American River, Southport, Broderick, Clarksburg, Davis). Perhaps triple-brooded. *Host Plant*: Leguminosae: *Robinia pseudoacacia* L., the usual host, is widely naturalized in sandy bottomlands in the Valley. Breeding has not been confirmed, but is almost certain.47. *Pyrgus scriptura* Boisduval. Least Checkered Skipper.Common to locally abundant on waste ground, roadsides, and levees, with the host plant; most often on compacted clay or alkali soils. Four to five broods, the first most contrastingly marked. *Host Plant*: Malvaceae: *Sida hederacea* (Dougl.) Torr.48. *Pyrgus communis* Grote. Common Checkered Skipper.Common to occasionally abundant throughout, usually in open country; especially numerous in agricultural land. Four or five broods, the cold weather specimens smaller, hairier, and whiter. *Host Plants*: Malvaceae: *Malva neglecta* Wallr.; *M. parviflora* L.; *M. sylvestris* L.; *M. nicaeensis* All.; *Althaea rosea* L.; *Sida hederacea* (Dougl.) Torr. (Note: *Pyrgus albescens* Plötz, the Common Checkered Skipper of southern California, has not been recorded from "northern or central California" (Tilden, 1965b), but its presence or absence in the Valley should be confirmed by genitalic examination of many males from a variety of localities.)

49. *Heliopterus ericetorum* Boisduval. Large Checkered Skipper.
Rare immigrant; both broods represented, but not known to breed in the Valley although a gravid female was taken in West Sacramento, v.5.73.
50. *Pholisora catullus* Fabricius. Sooty Wing.
Common, but seldom abundant, on waste ground, levees, and roadsides, often on compacted or alkali soils. Four or five broods. *Host Plants*: Amaranthaceae: *Amaranthus hybridus* L. preferred; *A. retroflexus* L.; Chenopodiaceae: *Chenopodium album* L.; *C. murale* L.; *Atriplex rosea* L.
51. *Erynnis persius* Scudder. Persius Dusky-Wing.
Frequent in sandy floodplains, as at Putah Creek and Willow Slough. Three (perhaps four) broods. *Host Plant*: Unknown; Leguminosae: *Lotus purshianus* (Benth.) Clem. & Clem. a possibility.
52. *Erynnis propertius* Scudder and Burgess. Propertius Dusky-Wing.
Infrequent in the Valley; mostly strays along the edges, but perhaps breeding along the American River where a very fresh specimen was taken iii.9.73. Flies only in spring.
53. *Erynnis tristis* Boisduval. Sad Dusky-Wing.
Common throughout, wherever planted or native oaks occur, and straying widely. Four broods. *Host Plants*: Fagaceae: *Quercus suber* L. (preferred at Davis, although introduced); *Q. lobata* Nee.; *Q. douglasii* H. & A.; *Q. wislizenii* A. DC. In all cases only tender new growth is eaten.
54. *Erynnis zarucco funeralis* Scudder and Burgess. Funereal Dusky-Wing.
Infrequent summer stray from the San Joaquin Valley, where resident. Not known to breed this far north.
55. *Hylephila phylaeus* Drury. Fiery Skipper.
Abundant in lawns, waste places, and sandy areas throughout. Five broods; cold weather specimens darker beneath. *Host Plant*: Gramineae: *Cynodon dactylon* (L.) Pers.
56. *Atalopedes campestris* Boisduval. Field Skipper.
Common; most numerous in sandy bottomlands, but straying widely. Four broods. *Host Plant*: Gramineae: *Cynodon dactylon* (L.) Pers.
57. *Ochlodes sylvanoides* Boisduval. Woodland Skipper.
Abundant in riparian forest; less common to infrequent elsewhere; absent in agricultural land. Not emerging until midsummer, but at least two broods. *Host Plants*: Gramineae: at Broderick, *Phalaris californica* H. & A. and *P. lemmonii* Vasey, perhaps other grasses.
58. *Ochlodes yuma* Edwards. Yuma Skipper.
Thus far recorded only at Stone Lake and Beach Lake in southern Sacramento County, in fresh-water marsh. Two broods. These records are the northernmost in the Valley; the species is widespread at Suisun Bay and in the Sacramento-San Joaquin Delta. *Host Plant*: Gramineae: *Phragmites communis* Trin. var. *Berlandieri* (Fourn.) Fern. (at Suisun Bay).
59. *Ochlodes agricola* Boisduval. The Farmer.
Rare stray along the streams from the foothills; not known to breed in the Valley.
60. *Polites sabuleti* Boisduval. Sandhill Skipper.
Abundant on sandy soils, as in river bottoms and on levees; widely distributed on waste ground and lawns in West Sacramento and Broderick, etc.; also in saline and alkali marshes; occasional elsewhere. Five broods, spring and fall specimens more heavily marked and often undersized, resembling the high-elevation subspecies *tecumseh* Grinnell. *Host Plants*: Gramineae: *Distichlis spicata* (L.) Greene; *Cynodon dactylon* (L.) Pers.
61. *Poanes melane* Edwards. Umber Skipper.
Frequent to common in riparian forest and levee thickets along the Sacramento and American Rivers; not seen elsewhere. Two broods. Host not known.
62. *Lerodea eufala* Edwards. Eufala Skipper.
Abundant throughout after late June, occasionally seen earlier; numbers variable from year to year. At least two broods. A buff-colored aberrant

was taken at Willow Slough, ix.4.72. *Host Plants*: Gramineae: *Cynodon dactylon* (L.) Pers.; *Sorghum halepense* (L.) Pers.; *S. bicolor* (L.) Moench.; *Setaria verticillata* (L.) Beauv.; *Echinochloa crus-galli* (L.) Beauv.; *Oryza sativa* L. The exact date when this southern species first entered the Valley is unknown, but it has been at Davis since the mid-1950s, at least.

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Table 1

Distribution of univoltinism in some

California butterfly faunas

Locality and Elevation:	Vaca Mts. (100-2500')	Contra Costa Co. (<3850')	Sacramento Valley ¹ (100')	Boreal Ridge (7000')	Marin- Sierra Camp (5000')
Number of species	65	84	62 (53)	70	63
Number of univoltines	25	27	14 (8)	47	38
Per cent univoltine	39%	32%	23% (13%)	67%	60%

¹The first number refers to the total fauna. The number in parentheses refers to breeding residents only. Immigrants are from the Vacas and Sierra foothills.

Table 2. Climatic Summary for Sacramento Airport Station, NWS.

Data from Dale, 1966. (For precipitation data, see Table 3)

Month	Temperature, °F					Relative humidity, % at 4 PM PST	% of possible sunshine	Mean sky cover in tenths, sunrise-sunset	Sunrise to sunset:			Mean number of days:			With heavy fog	With frost
	Normal		Extremes						Clear	Partly Cloudy	Cloudy	With rainfall	With heavy fog			
	Daily Max.	Daily Min.	Monthly	Highest	Lowest											
Jan.	53.2	37.2	45.2	66	23	73	44	7.0	7	5	19	10	10	14		
Feb.	58.6	39.8	49.2	76	28	62	60	5.9	10	5	13	9	6	2		
Mar.	64.8	42.0	53.4	80	31	53	69	5.5	10	8	13	8	2	1		
Apr.	71.4	45.3	58.4	91	34	45	79	4.6	13	9	8	5	0	0		
May	78.2	49.7	64.0	99	37	42	83	3.9	16	9	6	3	0	0		
Jun.	86.5	54.4	70.5	115	48	31	91	2.0	23	4	3	1	0	0		
Jul.	93.4	57.4	75.4	113	50	27	98	0.9	28	2	1	0	0	0		
Aug.	91.9	56.3	74.1	105	51	28	95	1.3	27	3	1	0	0	0		
Sept.	88.2	55.0	71.6	104	46	33	93	1.7	24	4	2	1	0	0		
Oct.	77.6	49.4	63.5	99	38	45	85	3.2	20	5	6	3	2	0		
Nov.	64.2	41.6	52.9	87	26	62	64	5.4	11	6	13	6	6	2		
Dec.	54.6	38.1	46.4	66	24	80	44	6.9	7	6	18	9	9	5		
Years of Record:	30	30	30	4	4	4	16	16	16	16	16	25	16	4		

Table 3. Normal total and maximum and minimum monthly and annual precipitation, Sacramento. Data from Figgins, 1971, which gives station and observer notes; covers period July 1849-July 1970.

<u>Month</u>	<u>Mean</u>	<u>Maximum and Year</u>	<u>Minimum and Year</u>
JAN.	3.58	15.04-1862	0.15-1889
FEB.	3.47	9.25-1940	0.04-1899
MAR.	2.46	10.00-1850	0.03-1956
APR.	1.62	14.20-1890	Trace-1949 [*]
MAY	0.62	3.25-1889	0 -1920 [*]
JUNE	0.12	1.45-1884	0 -1969 [*]
JULY	Trace	0.63-1860	0 -1970 ^{**}
AUG.	0.04	0.67-1953	0 -1969 ^{**}
SEPT.	0.22	3.62-1904	0 -1968 [*]
OCT.	0.80	6.85-1962	0 -1966 [*]
NOV.	1.54	11.34-1885	0 -1933 [*]
DEC.	3.55	13.40-1852	0 -1876
Annual	18.02	36.35-1852/53	4.71-1850/51

* indicates year is most recent of record; minimum has occurred in prior years.

** minimum has occurred in 50% or more of years of record.

Table 4. First flight dates of 25 common butterflies in the dry 1972 and wet 1973 seasons.

<u>Species</u>	<u>1972</u>	<u>1973</u>	<u>Difference</u>
<u>Vanessa carye</u>	ii.10	ii.7	(+3)
<u>Nymphalis antiopa</u>	ii.10	ii.7	(+3)
<u>Pieris rapae</u>	ii.26	i.20	(+37)
<u>Pyrgus scriptura</u>	iii.1	iii.24	(-23)
<u>Everes comyntas</u>	iii.3	iii.26	(-23)
<u>Pholisora catullus</u>	iii.3	iii.27	(-24)
<u>Strymon melinus</u>	iii.3	iii.9	(-6)
<u>Vanessa atalanta</u>	iii.4	ii.18	(+17)
<u>Phyciodes mylitta</u>	iii.4	iii.9	(-5)
<u>Plebeius acmon</u>	iii.4	iii.14	(-10)
<u>Atlides halesus</u>	iii.5	iv.3	(-29)
<u>Colias eurytheme</u>	iii.5	ii.25	(+11)
<u>Papilio zelicaon</u>	iii.5	iii.14	(-9)
<u>Papilio rutulus</u>	iii.6	iii.18	(-12)
<u>Pyrgus communis</u>	iii.7	iii.24	(-17)
<u>Vanessa cardui</u> (immigrant)	iii.8	ii.22	(+17)
<u>Euchloe ausonides</u>	iii.8	iii.2	(+6)
<u>Precis coenia</u>	iii.11	iv.3	(-23)
<u>Erynnis tristis</u>	iii.16	iv.8	(-23)
<u>Lycaena helloides</u>	iii.20	iv.29	(-40)
<u>Phyciodes campestris</u>	iii.23	v.2	(-39)
<u>Hylephila phylaeus</u>	iv.1	iv.12	(-11)
<u>Polites sabuleti</u>	iv.2	v.2	(-30)
<u>Limenitis lorquini</u>	iv.16	iv.27	(-11)
<u>Atalopedes campestris</u>	iv.19	v.5	(-16)

Mean departure from 1972 dates, 1973 -10.3

Table 5. Climatic comparison of 1971-72 and 1972-73 winters at Sacramento Airport Station, NWS.

1971-72								
	<u>Sept</u>	<u>Oct</u>	<u>Nov</u>	<u>Dec</u>	<u>Jan</u>	<u>Feb</u>	<u>Mar</u>	<u>Total</u>
Precipitation, inches	T	0.13	0.87	4.05	0.81	1.28	0.29	7.43
Mean high temperature, °F	88.7	76.1	64.7	50.7	48.5	61.0	71.6	65.9
Mean low temperature, °F	55.6	46.3	40.7	35.2	33.5	41.8	45.5	42.7
Mean monthly temperature, °F and deviation from normal	72.2	61.2	52.7	43.0	41.0	51.4	58.6	54.3
	+0.6	-2.3	-0.2	-3.4	-4.2	+2.2	+5.2	-0.3
Days below 32°	0	0	1	11	13	3	0	28
Days with precipitation >.01"	0	2	6	13	6	9	5	41
Days with heavy fog	0	1	5	12	15	8	1	42
% sunshine	95	86	79	54	48	64	89	73
Mean sky cover in tenths, sunrise-sunset	1.1	2.9	4.5	7.2	7.2	7.5	4.6	5.0
1972-73								
	<u>Sept</u>	<u>Oct</u>	<u>Nov</u>	<u>Dec</u>	<u>Jan</u>	<u>Feb</u>	<u>Mar</u>	<u>Total</u>
Precipitation, inches	0.90	1.75	5.14	1.88	6.87	5.64	2.76	24.94
Mean high temperature, °F	84.3	72.5	56.5	46.8	51.6	60.3	60.0	61.7
Mean low temperature, °F	54.6	51.5	42.8	34.3	37.0	45.9	42.2	44.0
Mean monthly temperature, °F and deviation from normal	69.5	62.0	49.7	40.6	44.3	53.1	51.1	52.9
	-2.1	-1.5	-3.2	-5.8	-0.9	+3.9	-2.3	-1.7
Days below 32°	0	0	0	13	18	0	0	31
Days with precipitation >.01"	3	8	14	11	17	16	11	80
Days with heavy fog	0	5	10	7	7	6	1	36
% sunshine	89	67	42	46	53	51	72	60
Mean sky cover in tenths, sunrise-sunset	2.6	4.9	7.6	6.2	6.7	8.2	5.9	6.0

Table 6

Host adaptations of Sacramento Valley butterflies

grouped by voltinism.

	<u>Monophagous</u>	<u>Oligophagous</u>	<u>Polyphagous</u>
Univoltine species	5	0	0
Multivoltine species	10	19	3
Totals	15	19	3

$$\chi^2 = 8.56$$

$$.025 > p > .010$$

[illegible]

Table 7.—Weekly occurrence of butterfly species in the Sacramento Valley in 1972 and 1973. No observations were made the weeks of April 16, July 30, and November 5.

NOTICES

Books on Lepidoptera: more than 300 books for sale. Free catalogue sent on request. Sciences Nat., 45 Rue de Alouettes, 75019, Paris, France

Wanted to make exchanges with collectors in California and Florida. Have Maylaysian butterflies for exchange (Trogonoptera brookiana, etc.) Masaki NAKAYAMA, Kitakyushu- Wakamatsu- Miyamaru -2-10-14, Fukuoka pref., Japan.

Need aid in preparation of specimens for study of population structure in butterflies; involves obtaining population samples, mounting, laboratory breeding, etc. Full or part time. Contact William Hovanitz, 1160 W. Orange Grove Ave. Arcadia, Calif. 91006.

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

Volume 13

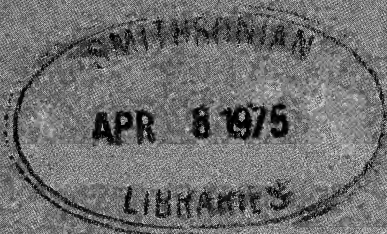
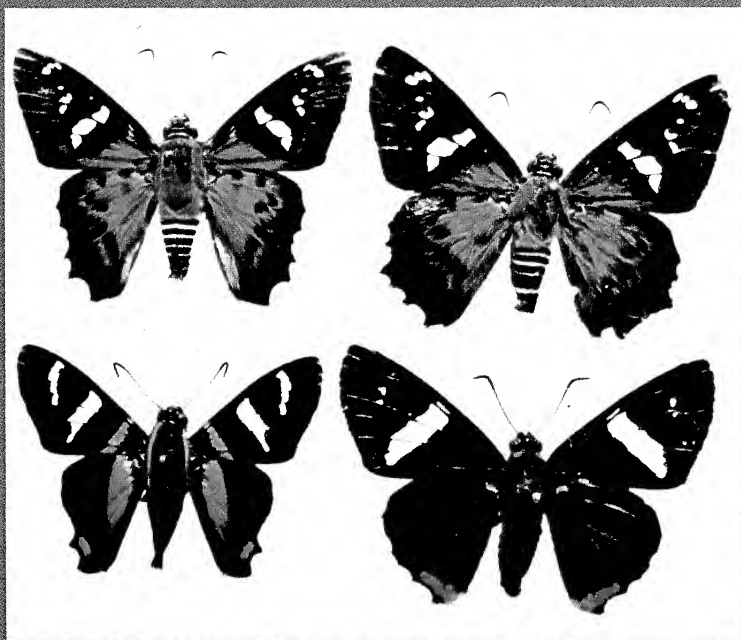
Number 2

June, 1974

IN THIS ISSUE

- The butterfly fauna of the
Sacramento Valley, California
Arthur M. Shapiro 73
- Extended flight periods of coastal and
dune butterflies in California
Robert L. Langston 83
- Habitat: *Brephidium pseudofea* (Lycaenidae)
John B. Heppner 90
- The early stages of various species of
the genus *Dirphia* (Saturniidae)
Brian O. C. Gardiner 101
- A new species of *Ormiscodes* (*Dirphiella*) from
Mexico (Saturniidae: Hemileucinae)
Julian P. Donahue and Claude Lemaire 123
- A new subspecies of *Euphydryas editha*
from the Channel Islands of California
Thomas C. Emmel and John F. Emmel 131

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STUDIES OF THE OVA AND FIRST INSTAR

LARVAE OF GEOMETRIDAE
(ENNOMINAE). I.

ROGER L. HEITZMAN¹

3112 Harris Avenue, Independence, Missouri 64052

ABSTRACT

Four species of the subfamily ENNOMINAE (*Pero marmoratus* Grossbeck, *Syssaura puber* Grote & Robinson, *Apicia confusaria* (Hubner) and *Tetracis crocallata* Guenee) are studied, and illustrations of setal maps, anal plates and head cases, and photographs of ova, are presented.

INTRODUCTION

THIS IS THE FIRST in a series of studies of the ova and first instar larvae of GEOMETRIDAE. It is hoped that these studies will provide further understanding of species, genus and sub-family relationships existing in the GEOMETRIDAE.

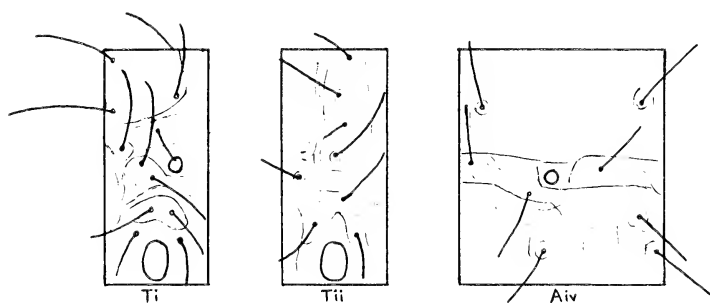
MATERIALS AND METHODS

Ova were secured by placing females in small vials containing paper tissue. I have found that most geometridae lay quite readily under these conditions, usually the very night they are captured.

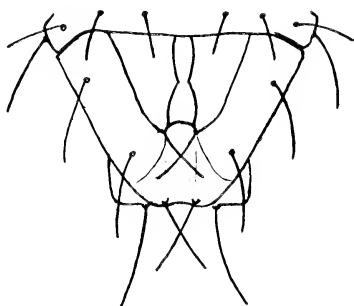
A WILD M-5 microscope with drawing tube attachment was used throughout the study. Photographs of ova were taken with phototube attachment and a Polaroid camera in conjunction with a double iris diaphragm for increased clarity.

The descriptions are based on ova and larvae from these female captures: *Pero marmoratus*, taken at Coolie Lake, Clay Co., Missouri, 3 May 1972; *Syssaura puber*, taken at Blue Springs State Park, Washington Co., Arkansas, 26 May 1972; *Apicia confusaria*, taken at Blue Springs State Park, Washington Co., Arkansas, 26 May 1972; *Tetracis crocallata*, taken at Warsaw, Benton Co., Missouri, 1 June 1972.

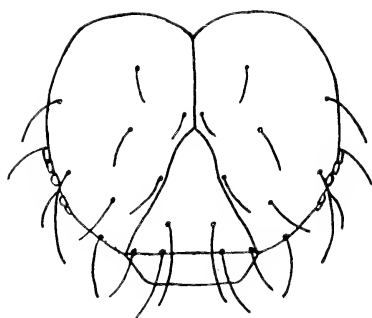
¹Research Associate, Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville.



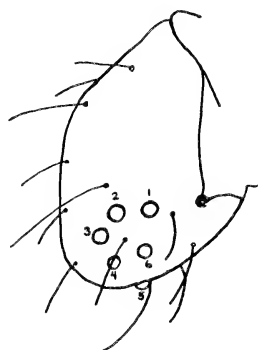
A



B



C



D

Fig. 1.—*Pero marmoratus* Grossbeck; (A) setal maps; (B) anal plate; (C,D) head, frontal and left lateral aspect, 80X.

RESULTS

Pero marmoratus Grossbeck

OVUM: Height: 0.82mm. Width: 0.65mm. Grass green with yellow areas. Laid singly and in groups on end or side. Eclosion in seven days.

FIRST INSTAR LARVAE: Length: approximately 4mm. Head very light brown, height: 0.38mm, width: 0.42mm. Dorsal surface: green with dark green bands encircling thoracic segments and fold between abdominal segments one through nine. Anal area yellowish green. Lateral surface: green. Anal as dorsal. Ventral surface: yellow green. Anal as dorsal.

Syssaura puber Grote & Robinson

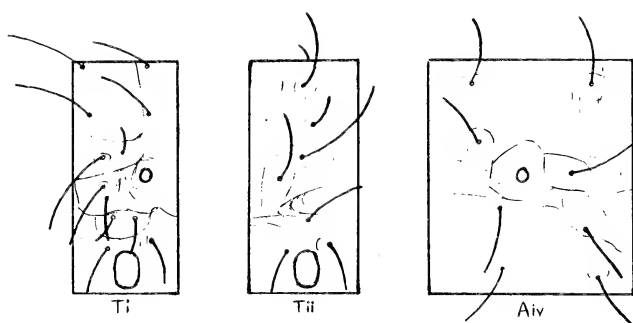
OVUM: Height: 0.74mm. Width: 0.58mm. Yellow changing to pale orange. Laid singly and in small groups on end or side. Eclosion in eight days.

FIRST INSTAR LARVAE: Length: approximately 3mm. Head very light yellow brown, height: 0.33mm, width: 0.36mm. Dorsal surface: thorax and last five abdominal segments yellow; first five abdominal segments light yellow. Dark brown square on first five abdominal segments. Lateral margins of squares joined by stripe running from first thoracic to eighth abdominal, paralleled by suprastigmatal brown stripes. Light brown band emerges from each square to encircle the body. Lateral surface: colors same as dorsal. First five abdominal stigma centered in a very dark brown irregular circle. A brown stripe joins each circle about the stigma. This stripe begins on first abdominal and ends on sixth abdominal. Ventral surface: colors same as dorsal. Dark brown square on the first five abdominal segments. A mid-ventral stripe joins the squares. Lateral margins of squares joined by stripes and paralleled by substigmatal stripes extending from first to sixth abdominal segments.

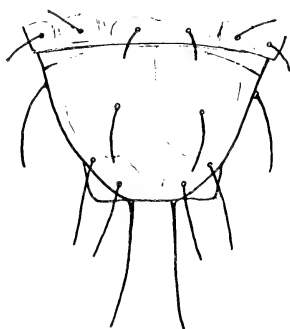
Apicia confusaria (Hubner)

OVUM: Height: 0.83mm. Width: 0.67mm. Green changing to dark golden brown. Laid loose without adhesive. Eclosion in ten days.

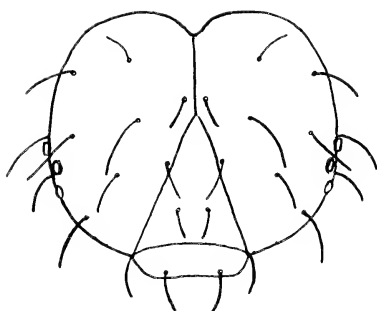
FIRST INSTAR LARVAE: Length: approximately 3mm. Head very dark brown almost black, height: 0.42mm, width: 0.38mm. Dorsal surface: first thoracic brown, second and third lighter with white blotches and markings. First six abdominal segments dark brown, last four lighter brown. First five abdominal segments with white V-shaped marking, base of V posteriorly oriented. White around base of setae of all abdominal segments. Lateral surface: thorax almost entirely white. Large white area



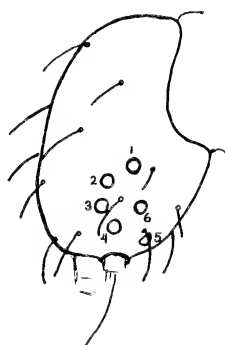
A



B

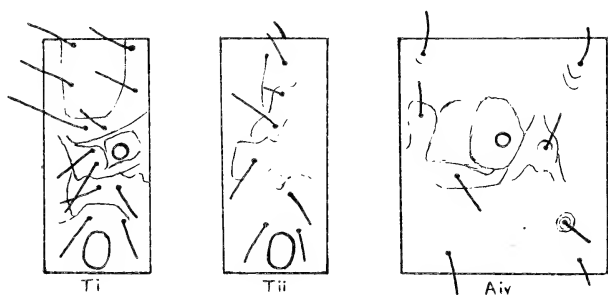


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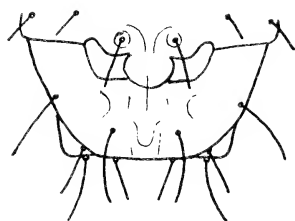


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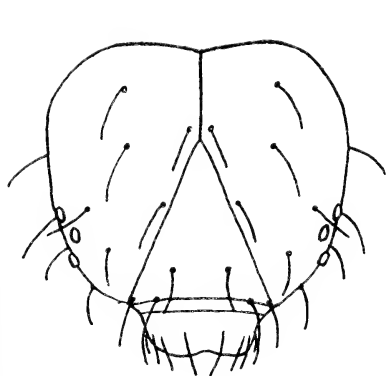
Fig. 2.—*Syssaura puber* Grote & Robinson; (A) setal maps; (B) anal plate; (C,D) head, frontal and left lateral aspect, 90X.



A



B



C



D

Fig. 3.—*Apicia confusaria* (Hubner); (A) setal maps; (B) anal plate; (C,D) head, frontal and left lateral aspect, 85X.

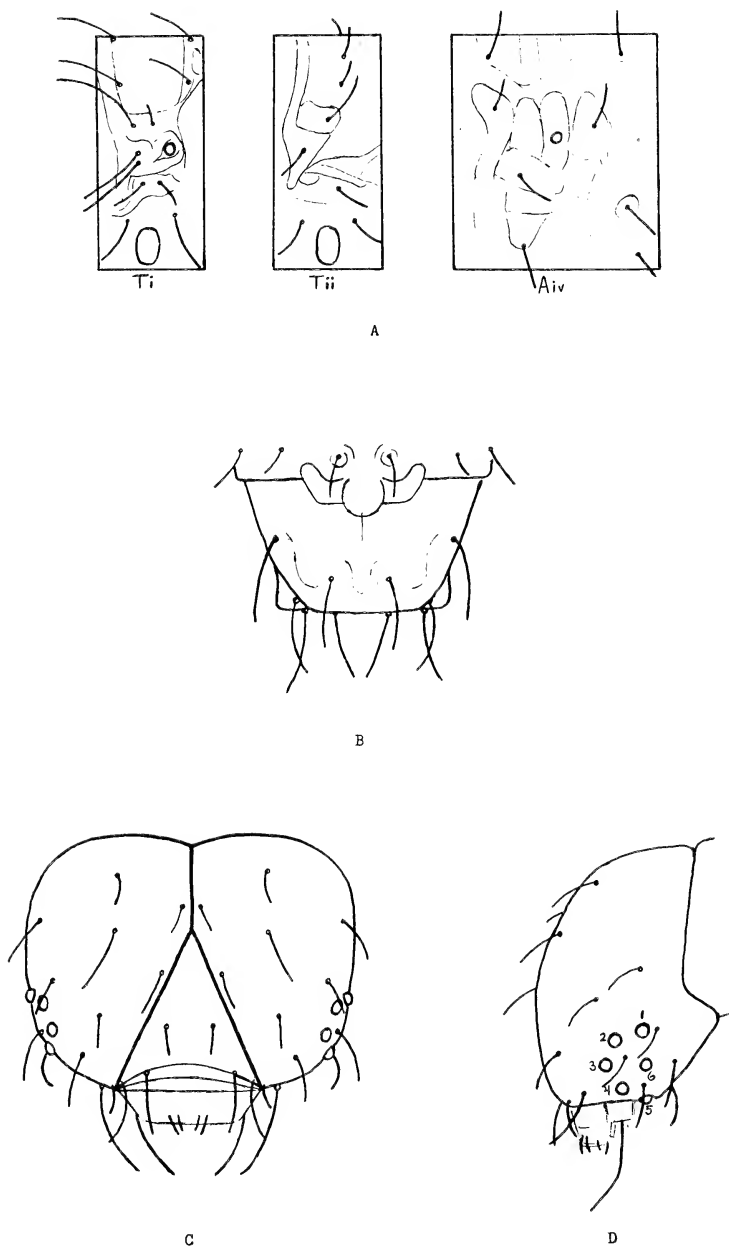


Fig. 4.—*Tetracis crocallata* Guenee; (A) setal maps; (B) anal plate; (C,D) head, frontal and left lateral aspect, 90X.

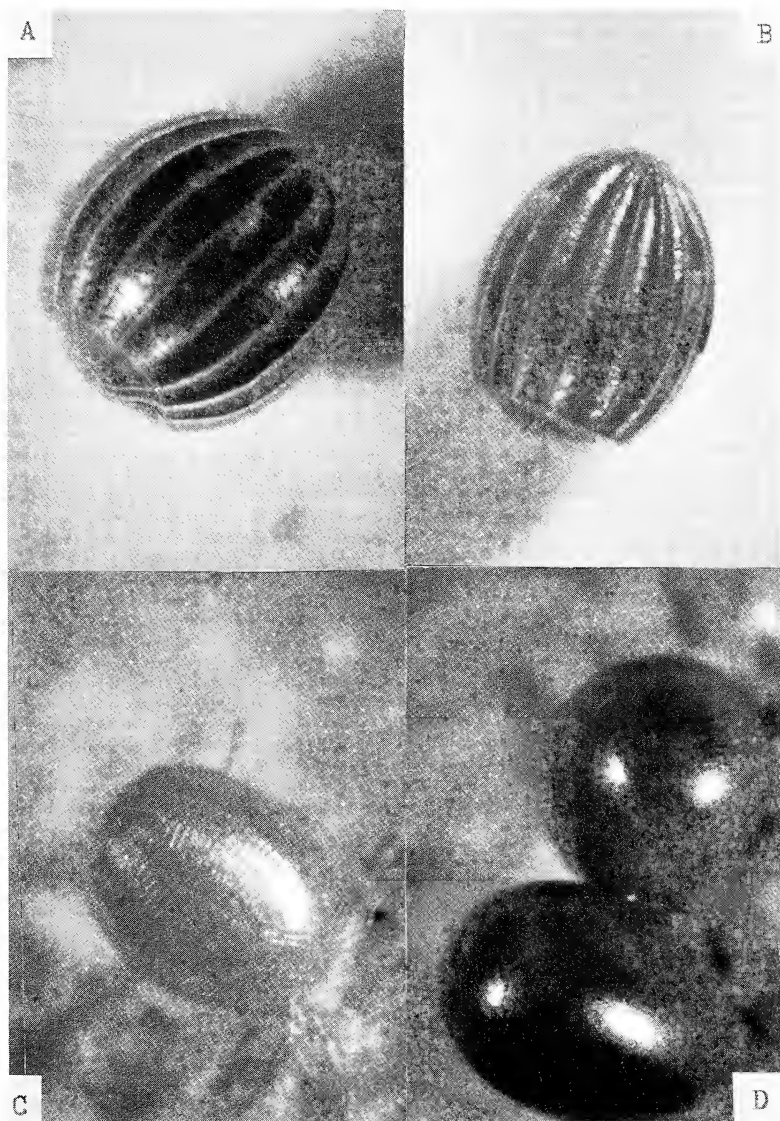


Fig. 5.—Ova; (A) *Tetracis crocallata*; (B) *Apicia confusaria*; (C) *Syssâura puber*; (D) *Pero marmoratus*, all 50X.

in center of each abdominal segment where setae are located. Abdominal colors same as dorsal. Ventral surface: thorax white and light brown. First five abdominal segments with white blotches and striations. Sixth abdominal segment with two white dashes. Abdominal colors same as dorsal.

Tetracis crocallata Guenee

OVUM: Height: 0.90mm. Width: 0.82mm. Very deep green. Laid loosely without adhesive. Eclosion in eleven days.

FIRST INSTAR LARVAE: Length: approximately 3mm. Head very dark brown almost black, height: 0.36mm, width: 0.42mm. Dorsal surface: thorax dark brown, second and third segments with white blotches and markings. First six abdominal segments very dark brown almost black; last four segments brown. First five segments with white heart-shaped marking, bottom of heart posteriorly oriented. Last four segments have some vague creamy patterns. Lateral surface: thorax mostly white except for first segment which is mainly dark brown. Large white area in center of each abdominal segment where setae are located. Area is creamy yellow on last five segments. Abdominal colors same as dorsal. Ventral surface: thorax white and brown. First five abdominal segments with white blotches and striations. Abdominal colors same as dorsal.

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ALTITUDINAL MIGRATION OF CENTRAL CALIFORNIA BUTTERFLIES

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BUTTERFLY SPECIES WHICH ARE NOT MASS MIGRANTS in the sense of the Monarch (*Danaus plexippus* L., Danaidae) or the Painted Lady (*Cynthia cardui* L., Nymphalidae) nonetheless are often recorded as "strays" far beyond their usual ranges. Such "strays" may be geographic or altitudinal. The occurrence of individual "strays" could reflect active or passive dispersal which could be density-related or not. In a previous paper (Shapiro, 1974b) data were presented on lowland California butterflies collected at 5000 and 7000 feet above sea level in the central Sierra Nevada in 1972. It was noted that several of the species displaying altitudinal dispersal in California are well-known northward dispersers on the Atlantic coastal plain in the eastern United States. Regular collections of butterflies and skippers were made at Donner Pass, Placer County, California, elevation approximately 7000 feet, from 27 June to 16 October 1973, and from 31 May to 16 October 1974. In the course of this work, several additional records of altitudinal dispersal were obtained, as reported below. In all of these cases, the insects appear to have dispersed upslope. In addition, some evidence suggesting downslope dispersal by one species, *Nymphalis milberti* Latreille (Nymphalidae), is presented.

Donner Pass Records

Donner Pass is well documented, thanks to assiduous collecting by Emmel and Emmel (1962a, b; 1963a, b; 1974) and appears to have the richest butterfly fauna of any investigated montane area in temperate North America of comparable size—about 100 species in a four-square-mile area. The geography and vegetation of Donner Pass are discussed by Emmel and

Emmel (1962a), who note that part of its richness stems from the mixture and overlap of east-slope (Great Basin) and west-slope (Californian) biotic elements. In evaluating the significance of altitudinal dispersal at Donner, it is often difficult—or impossible—to decide whether the immigrants are from the east or west slope. The descent to the lowlands is much more precipitous on the east slope, which is also less heavily forested, so that dispersal (especially if aided by thermals) may be much more rapid from the east.

The records which follow do not exhaust the list of potential dispersers: only especially striking examples are enumerated. LYCAENIDAE: *Brephidium exilis* Boisduval. A female Pygmy Blue in good condition was taken 5 October 1973 feeding on the flowers of *Chrysothamnus nauseosus* (Pall.) Brit. (Compositae) about 1000 feet east of Norden. *B. exilis* occurs abundantly on the floor of the Sacramento Valley at the western base of the Sierras, and has been taken up to about 2800 feet in the foothills in El Dorado County and at 4600 feet in Nevada County. It is also common on the Great Basin floor east of Sierraville in late summer and in desert conditions near Reno, Nevada. Colonization could thus occur from either side of the mountains. Among potential hosts of *B. exilis* (Shapiro, 1973) only the introduced weed *Salsola kali* L. var. *tenuifolia* Tausch. (Chenopodiaceae) occurs at Norden, along with two other undetermined Chenopods.

Leptotes marina Reakirt. A male in excellent condition was taken by S. R. Sims on *C. nauseosus* flowers at the Donner Lake overlook on the Norden-Truckee road, 28 September 1973. This blue also occurs at low elevations on both sides of the Sierra. It is, however, very local in the Sacramento Valley as compared with the Great Basin and seems much more likely to have reached Donner Pass from the east than the west. A female *L. marina* was taken at Tahoe City, 18 miles south of the Pass at the same elevation, on 24 September 1974. Tahoe City has a very marked east-slope character.

Lycaena helloides Boisduval. The Purplish Copper is a fairly frequent capture in the mid-elevation Sierras. In 1973, three males were taken at Donner, on 17 August, 13 September, and 16 October. In 1974, single males were taken on 26 June and 24 July. The 16 October, 1973 specimen was taken on *C. nauseosus* flowers at the same spot where *B. exilis* was found the previous week. *L. helloides* is common in the lowlands on both

sides of the Sierran massif. Potential host plants (Polygonaceae) are numerous at Donner. On the west slope, *L. helloides* becomes sporadic above about 2500 feet, but in 1974 it was found breeding at Lang Crossing, Nevada County, at about 4600 feet. *Habrodais grunus* Boisduval. One female, 18 July 1973, on the Lake Mary road. This is characteristically a species of the upper foothills and through the Transition Zone, always associated with its host, *Quercus chrysolepis* Liebm. (Fagaceae). This tree is rarely seen above about 5000 feet at the latitude of Donner Pass and has never been observed in the Pass area. The specimen must have reached Donner from the west.

NYMPHALIDAE: *Limenitis bredowii californica* Butler. Emmel and Emmel (1974) report three females, 21 June 1970. Individuals (sex undetermined) were seen at Donner Pass on 11 July and 28 September 1973, and on 9 June, 24 July, and 16 October 1974. It thus appears that *L. b. californica* reaches Donner fairly frequently, but its breeding status is unknown. It is a very strong-flying species which is common to at least 5000 feet on the west slope.

Precis coenia Hubner. In 1972, this was seen only once at 7000 feet (Boreal Ridge). In 1973, specimens were seen or taken on 11 and 25 July, 17 August, 28 September, and 5 and 16 October at Donner. In 1974, it was not seen at Donner at all. Emmel and Emmel considered it common at Donner in 1960. Hosts (Scrophulariaceae, Plantaginaceae) are numerous and it seems very likely that it breeds in years when gravid females arrive before late summer. The Buckeye is abundant on the floors of the Sacramento Valley and Great Basin, and it breeds every year on the west slope to about 3000 feet.

HESPERIIDAE: *Hylephila phylaeus* Drury. Females: Soda Springs, 28 September 1973, and Norden, 5 October 1973, the latter on flowers of *C. nauseosus*. The Fiery Skipper is extremely abundant in the lowland Sacramento Valley, and locally so around Reno in the Great Basin. In 1972 it was taken once at 5000 feet on the west slope (female, 29 September). Immigration from the west seems more probable for this species.

Atalopedes campestris Boisduval. One of each sex taken at Norden, 24 July 1974. It seems very unlikely *a priori* that this lowland species breeds or overwinters at Donner Pass. It is common in the Sacramento Valley and unknown at Truckee.

Donner Pass may be an exceptionally good accumulator of altitudinal dispersers for topographic and meteorological reasons. The Pass is noted for its high winds throughout the year, which occur when barometric pressure is significantly higher on one side of the range than on the other and the denser air rushes through the Pass to displace the lighter air across it. The direction of this flow is more often from west to east than the reverse. In autumn, however, Canadian high pressure may build into the Great Basin and produce sustained easterly flow for several days.

Movements of *Nymphalis milberti*

In general, records of altitudinal dispersers are of lowland species at high elevations rather than the reverse. Similarly, in the eastern United States, many more butterflies appear to disperse northward than the reverse. The Tortoiseshells, genus *Nymphalis*, provide exceptions to this generalization. In the east, *N. milberti* Latreille and *N. j-album* Bdv. & LeC., while basically northern, undergo periodic range extensions which carry them far to the south of their permanent breeding grounds, and to lower elevations. This occurs on a much larger scale in the mass-migratory *N. californica* Bdv. (Shapiro, 1974a).

Nymphalis milberti is generally a rare insect in central California. Garth and Tilden (1963) report it from Transition Zone up to 13,090 feet in Yosemite. Transition Zone, the zone of yellow pine, incense cedar, and Douglas fir, has its lower limit around 3000 feet.

On 11 April 1973, a female *N. milberti* was taken at the Spenceville Recreation Area, Yuba County, at an elevation of about 1000 feet. It was found in a colony of the introduced nettle, *Urtica urens* L., at the edge of a picnic area in cottonwood-willow forest along Dry Creek.

On 6 April 1974, a female *N. milberti* was taken in North Sacramento, Sacramento County, at an elevation of about 20 feet. It was on flowers of wild radish, *Raphanus sativus* L., at the edge of riparian cottonwood forest with an extensive understory of *U. urens*; the native *U. holosericea* Nutt. is also present. With the *N. milberti* were several *Vanessa atalanta* L., and larvae of this species were found on the native nettle. It is noteworthy that in both lowland records of *N. milberti* the colony of *U. urens* was the only occurrence of this plant for many miles in all directions. The close association of two females with such plants suggests at least a significant possibility of breeding at low elevations in spring.

As a working hypothesis it may be proposed that *N. milberti*, like *N. californica*, may overwinter and rear a spring brood at low elevations, disperse upslope for summer breeding, and return to the lowlands in autumn. Because of its scarcity, this movement could easily escape notice in normal years.

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THE CHROMOSOMES OF
APANTESIS PHALERATA, *A. RADIAN*S,
AND THEIR HYBRID

IN FLORIDA POPULATIONS (ARCTIIDAE)¹

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Gainesville 32601

OCCURRING WIDELY in the southeastern portion of North America are two very similar and commonly confused species of *Apantesis*, or "tiger moths." *Apantesis phalerata* (Harris), a more broadly distributed moth, has recently been shown in northern Florida populations (Bacheler, 1972) to be specifically distinct from *A. radians* Walker in several biological and morphological characters. The adults of these two species and their hybrid are illustrated in Fig. 1. We wish to report here the surprising differences in chromosome numbers between the two closely related species, and their experimentally-produced hybrids. These chromosome counts represent the first published data for species in this arctiid genus.

METHODS

Meiotic divisions in the Lepidoptera are most easily observed in testes of male adults (Emmel, 1969) but spermatogenesis was essentially completed in almost all *Apantesis* adults examined. Further preliminary studies showed that germ cell division in *A. phalerata* and *A. radians* occurred to the greatest degree during the penultimate instar of male larvae. Thus the standard procedure for chromosome preparations previously reported (Emmel, 1969) was modified as follows.

Testicular tissues of late penultimate *A. phalerata*, *A. radians*, and *A. phalerata* ♀ X *A. radians* ♂ hybrid larvae were fixed by injecting a 3:1 absolute ethyl alcohol : glacial acetic acid mixture into the sixth abdominal segment with a no. 27 hypodermic syringe. The injected larvae were placed into four ounce jars containing the same fixative, labeled, and refrigerated at about -20°C for later dissection.

¹Fla. Agricultural Experiment Station Journal Series No. 4560.

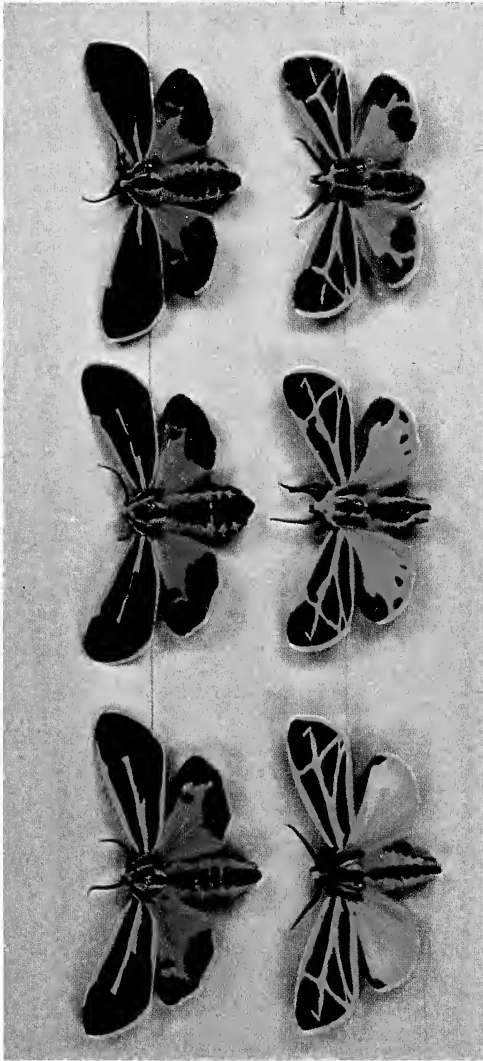


Fig. 1.—Males (lower specimens) and females of *Apantesis phalerata* (left), *A. radians* (right), and their hybrid (center).

For chromosome study the testes, usually found in the dorsal area of the sixth abdominal segment of male larvae, were removed with No. 5 watchmaker's forceps and placed onto a standard microscope slide. The testes were then macerated and a few drops of Lacto-Aceto-Orcein Stain (Emmel, 1969) added. This preparation was allowed to stand for about 10-12 min. The stained testes were next covered with a coverslip and the preparation squashed with about 400 lb/in.² pressure between two pieces of blotting paper. The perimeter of the coverslip was then sealed with clear lacquer.

Slides were inspected with a Zeiss Research Microscope STANDARD WL fitted with 25X and 40X plan-apochromatic field objectives. An oil-immersion Planapo 100X objective was used for critical observations.

Chromosome counts were made during meiotic division I when chromosomes were paired in synapsis. Photographs were taken of unusually clear chromosomes sets and of any interesting anomalies.

All larval material was reared in the laboratory from wild females of both species collected in populations in the vicinity of Gainesville, Alachua County, Florida. Hybrid larvae were obtained from laboratory crosses of virgin adults of the two species.

RESULTS AND DISCUSSION

Definitive chromosome counts with photographic confirmation were obtained from microscopic slide examination of *phalerata*, *radians*, and hybrid larval testes squashes. The apparent haploid chromosome numbers of *phalerata*, *radians*, and the hybrid cross are $n = 29$, 30, and 29 respectively (Fig. 2). Since no other counts have been reported in the genus the interpretation of the chromosomal evidence for the phylogenetic relationship between these two species is necessarily limited and speculative. However, there are two principal ways in which a difference in lepidopteran chromosome numbers of this type may be explained and some evidence exists to indicate which hypothesis is more tenable.

1. Reduction in Number by Fusion or Loss

The karyotypic origin of *phalerata* ($n = 29$) could have resulted from the fusion of two of *radians*' (or an ancestor of *radians*) 30 chromosomes, or a loss of one ancestral chromosome. A reduction in chromosome number from a characteristic

lepidopteran haploid set of 31 is not infrequent in the arctiids and closely related noctuids; in counted species of both families the mean haploid number is 31 chromosomes (Robinson, 1971). The reported arctiid counts show one species with a haploid number of 26, four with 28, one with 29, two with 30, seventeen with 31, and one species with a number varying between 30 and 33. The noctuids show the same apparent tendency toward reduction in chromosome number for the probable ancestral number of 31, with seven species having less than 31 and three exceeding 31.

Thus it is possible that *radians* resulted from the fusion of two chromosomes in an $n = 31$ ancestor, and that *phalerata* was the result of a further fusion of two *radians* chromosomes. These fusions would reduce slightly the amount of possible genetic recombination and thus the general adaptive flexibility of the species. But fusion would be an evolutionarily favorable event for a well adapted species where the need for genetic recombination would be minimally valuable, even selectively disadvantageous.

If *phalerata* had indeed evolved with fusion from an ancestor with a haploid number of 30, such as *radians*, microscopic examination of its 29 chromosomes might show one double-sized or exceptionally large chromosome. However, photographic examination did not disclose a significantly larger chromosome. Thus it seems more probable that loss of a chromosome from the *radians* complement or loss of two chromosomes from a common ancestral complement represents a plausible explanation of the origin of *phalerata's* $n = 29$ set of chromosomes.

2. Hypothesis Involving Increase in Number by Fission (Fragmentation)

The possibility also exists that *phalerata* (or an $n = 29$ ancestor of *phalerata*) gave rise to *radians* (or an ancestor of *radians*) by fragmentation of one of its chromosomes. The evolution of many lepidopteran species has been accompanied by an increase in chromosome number (Emmel, 1972; Emmel and Trew, 1973). Thus, one of *phalerata's* 29 chromosomes could have split, with both parts being retained in the new genotype, resulting in a new chromosome complement of 30. The selective advantage of this fragmentation would be increased potential for genetic recombination, allowing the species to be more generally adaptable. (Naturally, the ancestral number of 29 in *phalerata* would likely have been derived originally by reduction through loss or fusion.)

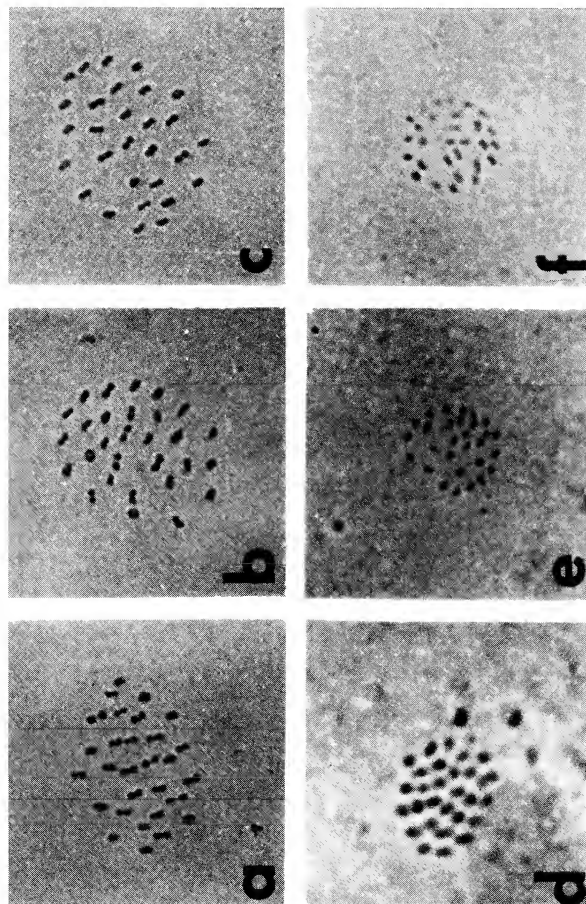


Fig. 2.—Photomicrographs of testes squashes at 1110X magnification; chromosomes in metaphase during first meiotic division. (a-c) *Apantesis phalerata*, F₁ brood L-60 ($n = 29$); (d) *A. radicans*, F₁ brood D-62 ($n = 30$); (e,f) *A. radicans* ♂ x *A. phalerata* ♀, brood DL-6261 ($n = 29$).

There is some support for the above fragmentation hypothesis in *phalerata* and *radians*. If *radians*' karyotype had resulted from the fragmentation of one of the ancestral *phalerata* (or similar $n = 29$ species) chromosomes, two smaller chromosomes might be found among the 30. Two *radians* chromosomes (Fig. 2d) do appear smaller than the others.

If *radians* had evolved from *phalerata*, one probably would expect *radians*' range to be more restricted, having split off rather recently (suggested by their almost identical morphology, life history, and occasional laboratory hybridization). Such is the case, with *radians* occupying about a third the area that *phalerata* does.

EVIDENCE FROM THE HYBRIDS OF THE TWO SPECIES

If one accepts the ancestral fragmentation hypothesis as more likely, the hybrid chromosome number of 29 is most easily explained by the two short chromosomes of the *radians* parent pairing with their "former" chromosome from the *phalerata* parent in the hybrid larvae testes (at meiosis I). A uniform count of 29 in meiosis II cells of the hybrid larvae would result from the loss of one of the two small chromosomes after pairing in meiosis I (the loss of both small chromosomes would have meant the probable additional loss of the unpaired *phalerata* chromosome, resulting in a hybrid count of 28, or at least a variable count of 28 and 29 in meiotic (II) cells of the hybrid adult).

If one follows the ancestral fusion hypothesis (Section I), the picture in the hybrid would be superficially similar ($n = 29$ at meiosis I), only the two complete chromosomes of the *radians* parent would pair with the large, "fused" chromosome of the derivative *phalerata* parent in the hybrid larval testes cells. The testes of such a hybrid male larva should have a variable number of chromosomes (28 or 29) in meiotic cells, or if all cells were $n = 29$ (due to the loss of just one *radians* parental chromosome), about half the cells in meiosis II should have one chromosome noticeably smaller than the other 28 and half the cells should have all 29 chromosomes appearing as uniformly-sized.

Unfortunately, our material did not provide sufficient plates of material in meiosis II to ascertain whether such a chromosomal loss was indeed the case.

SUMMARY

Apantesis phalerata and *A. radians* are two closely related, phenotypically similar arctiid species found sympatrically in northern Florida. Examination of meiotic divisions in testes of penultimate instar larvae indicated that the haploid chromosome numbers for the two species are different: $n = 29$ for *phalerata* and $n = 30$ for *radians*. Their hybrid has a chromosome number of $n = 29$. These are the first cytological observations reported from the genus *Apantesis*.

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A PARTIAL BIBLIOGRAPHY OF THE WORLD DISTRIBUTION AND ZOOGEOGRAPHY OF BUTTERFLIES

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INTRODUCTION

THIS BIBLIOGRAPHY (albeit incomplete) is intended as a guide to the world's geographical distribution of butterflies, with emphasis on broader, more comprehensive works. Additional sources of major importance are contained in *Lepidopterorum Catalogus*, *Das Tierreich*, *Genera Insectorum*, Seitz' *Macrolepidoptera of the World*, *Zoological Record* (Insecta), and "Recent Literature on Lepidoptera" series in *Lepidopterists' News* (= *Journal Lepidopterists' Society*). Perhaps others will contribute further to the task of completing a thorough listing.

With the past decade of a major revolution in geology, "continental drift" has reappeared in the form of plate tectonics and sea-floor spreading. Butterflies are such a well-studied group zoogeographically that their distributional patterns eventually may be illuminated by the new ideas from geology (e.g. see Holloway, 1969). This bibliography was compiled in conjunction with my own studies (in progress) of the biogeography of organisms and plate tectonics, and is offered as an aid to others engaged in zoogeographical work.

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THE NOMENCLATURE IN AN IMPORTANT BRITISH CHECK LIST (1972) PART 2: CORRECTIONS OF FAMILY-GROUP NAMES FOR GEOMETRIDAE (LEPIDOPTERA)

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A COMPARISON OF THE SECOND EDITION with the original Check List by Kloet and Hincks (1945) reveals among other things great differences in names used for subfamilies of *Geometridae*:

First Edition

Second Edition

(1945)

(1972)

No. 53 *Geometridae*

No. 13 *Brephidae*
(= *Monocteniidae*)
No. 11 *Geometridae*
No. 10 *Sterrhidae*
No. 12 *Hydriomenidae*
No. 14 *Selidosemidae*

: *Archiearinae*
: *Oenochrominae*
: *Geometrinae*
: *Sterrhinae*
: *Larentiinae*
: *Ennominae*

As long ago as 1844, Duponchel divided his tribe *Phalénides*, i.e. *Geometridae* sensu lato, into 18 subtribes (I-XVIII). The *Phalénides* of Duponchel, however, did not include *Brephos* Ochsenheimer, 1816, a genus dealt with by him, Duponchel, as pertaining to another tribe, namely *Phalénoides*.

Duponchel's subtribes *Chlorochromites* (II) and *Acidalites* (XVI) correspond to the modern subfamilies *Geometrinae* and *Sterrhinae* (= *Scopulinae*) respectively, while *Eubolites* (X), *Cidarites* (XI), *Larentites* (XII) and *Melanthites* (XIII) do all to the modern *Larentiinae*.

The modern *Selidosematinae* = *Ennominae* = *Boarmiinae* were disposed by Duponchel in not less than 12 subtribes: *Ennomites* (I), *Gnophites* (III), *Boarmites* (IV), *Cléorites* (V), *Amphidasites* (VI), *Hibernites* (VII), *Fidonites* (VIII), *Aspilatites* (IX), *Zérérites* (XIV), *Cabérites* (XV), *Sionites* (XVII), and *Dasydites* (XVIII). Of these *Ennomites* and *Boarmites* survived alone and changed later to *Ennomidae/Ennominae* and *Boarmiidae/Boarmiinae*, these being recognized as two distinct family-groups up to the time of Packard (1876). Since both divisions have been united thereafter, *Ennomites* and *Boarmites* became equally old nomenclatorial rivals (Article 23d).

ARCHIEARINAE

Type-genus (subfiliotype): *Brephos* Ochsenheimer, 1816 (nec Huebner, 1813, Samml. exot. Schmetterl. 1, pl. 90!). Replaced as junior homonym by *Archiearis* Huebner, 1823. Hence the change of *Brephinae* to *Archiearinae*.

OENOCHROMATINAE

Type-genus (subfamiliotype): *Oenochroma* Guénée, 1857. This subfamily is often wrongly named '*Oenochrominae*' (oeno-chroma, -tos), instead of *Oenochromatinae*. *Monocteniidae*, based on *Monoctenia* Guénée, 1857 would be a junior synonym of *Oenochromatinae*.

GEOMETRINAE

Type-genus (subfamiliotype): *Geometra* Linnaeus, 1758 (validated as of this date under suspension of the Rules—see Opinion 450).

SCOPULINAE

Type-genus (subfamiliotype): *Acidalia* Treitschke, 1825 (nec Huebner, 1819). The oldest valid name of this genus is *Scopula* Schrank, 1802. Accordingly, the family-group name *Acidaliinae* has been replaced by *Scopulinae*, as proposed by Hampson (Hampson and Durrant, 1918).

LARENTIINAE

Type-genus (subfamiliotype): *Larentia* Treitschke, 1825. The family-group name *Hydriomeninae* must be sunk as a junior synonym of *Larentiinae*.

BOARMIINAE

Type-genus (subfamiliotype): *Boarmia* Treitschke, 1825. Since *Ennomites* and *Boarmites* have been published simultaneously (Duponchel, 1844), their relative priority is determined by the action of the first reviser, viz. Hampson (1898?) to whom the modern concept of *Boarmiinae* has been attributed (Hering, 1932). *Ennominae* as conceived by Dyar (1903), as well as *Selidosematinae*, based on *Selidosema* Huebner, 1823 and proposed first as a family-group name by Meyrick ('*Selidosemidae*') seem not to be more than junior synonyms of *Boarmiinae*.

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ILLUSTRATIONS AND DESCRIPTIONS OF
SPECIES OF SOME PYRRHOPYGINAE
FROM PANAMA (HESPERIIDAE)

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THE PAST TEN YEARS' COLLECTING in the Republic of Panama and in the Canal Zone have produced new information on previously described species of the HESPERIIDAE and a number of new species (Nicolay & Small, 1969 and Nicolay, 1973). The purposes of this paper are to describe new sub-species in the genera *Zonia* and *Myscelus*, provide additional notes on species already named, and to illustrate species not figured previously.

***Zonia zonia panamensis* Nicolay, new subspecies**

Figures 1f, 2f, 5, 6, 7

Male: Length of forewing, 29 mm. Upperside: forewing black, a discal row of conjoined white hyaline spots from vein 1 through cell to coastal margin in spaces 11 and 12, the latter as narrow streaks, but triangular in interspace 1b, rectangular in space 2, almost square across cell; a narrow, small triangular white hyaline spot in interspace 3, the apex not reaching vein 4; white hyaline apical spots in spaces 4 and 5, three smaller spots across the upper edge of spot in space 5 in spaces 6, 7 and 8. A narrow bluish-white basal band from costa to inner margin, another pale blue parallel sub-basal band from costa to inner margin continued as a broken blue bar in space 1a to termen, then as a sub-marginal blue line to spot in space 3 with a few blue scales toward apical spot in space 5. Hindwing black, upper and lower bluish-white basal streaks, separate and not reaching the central white hyaline band which is 1 mm wide, extending from vein 2 into interspace 7, but not reaching vein 8; a submarginal bright blue macular band from interspace 1b to vein 7. Fringes dark brown. Underside: forewing dull black, hyaline markings of the upperside repeated in like manner; sparse pale blue scaling at wing base; a scattering of blue scales submarginally from end of spot in space 3 to inner margin. Hindwing black, inner margin blue-scaled; a sub-basal blue-white band from mid vein 1 to costa; central hyaline band as on upperside with an added double blue spot in space 1c; submarginal macular blue band narrow, broken outward at vein 4, widening toward costal margin. Fringes white, checked brown at each vein end. Palpi and forecoxae white stripped; head and patagia white spotted; thorax with 4 bluish-white stripes; abdomen with alternate bluish-white and black bands; anal tuft dark brown.

Female: Unknown.

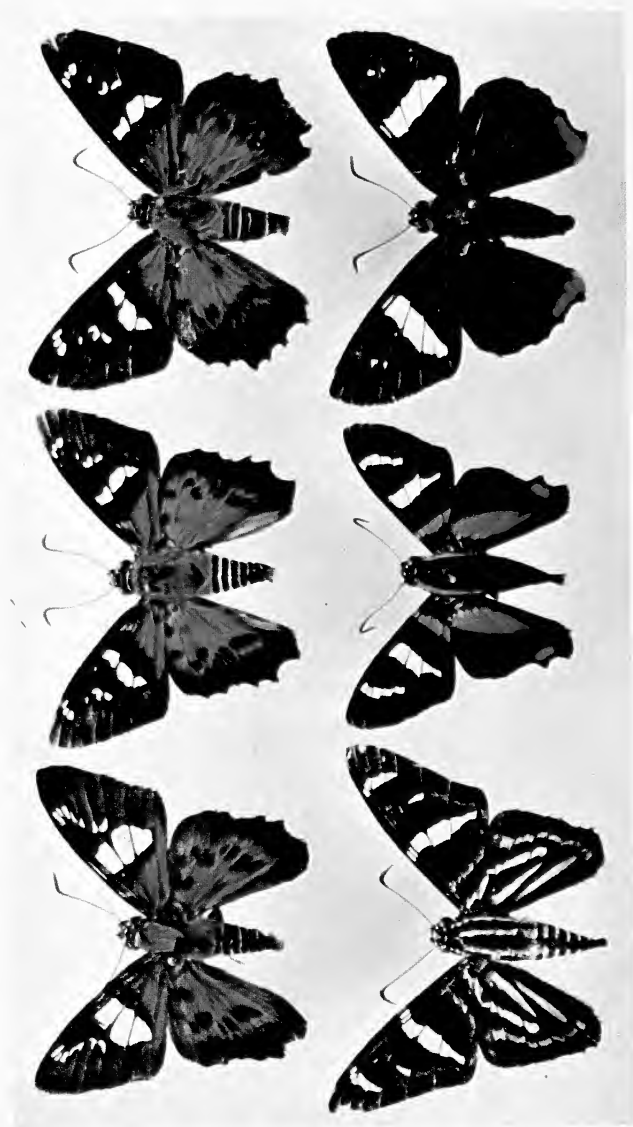


Fig. 1. — Upper row, left to right (a) *Myscelus assaricus michaeli* Nicolay allotype ♀, Madden Forest Preserve, Canal Zone; (b) *Myscelus assaricus michaeli* Nicolay, holotype ♂, Madden Forest Preserve, Canal Zone; (c) *Myscelus assaricus mapiri* Strand ♂, Rio Songo, Bolivia 750 m.; Lower row, left to right (d) *Aspitha leander* Boullet ♀, Gatun, Canal Zone; (e) *Aspitha leander* Boullet ♂, Gatun, Canal Zone; (f) *Zonia zonía panamensis* Nicolay, holotype ♂, Madden Forest Preserve, Canal Zone.

Correction: (Fig. 1 and 2); Left and right reversed.

In place of 'left to right', please read 'right to left'.



Fig. 2. — Upper row, left to right; underside of the same species as illustrated in figure 1.
Lower row, left to right; underside of the same species as illustrated in figure 1.

Holotype male, Madden Forest, Panama Canal Zone, 6 Feb. 1968, collector, S. S. Nicolay. Paratypes, same locality; 1 ♂ 15 Aug. 1968, 1 ♂ 15 Dec. 1968, 1 ♂ 23 July 1969, 1 ♂ 24 July 1969, G. B. Small, collector. The holotype will be deposited in the American Museum of Natural History, New York, New York, the paratypes, in the collections of the author and Mr. G. B. Small.

Panamensis has been one of our most interesting catches in the Canal Zone in recent years. Evans (1951) described the nominate species *zonias* for which he erected the genus. Known only from the single male type taken at Teffe (Ega) Amazonas in 1879, it has not been figured previously. Photographs of the type, (Figures 3 & 4) were provided by Mr. R. E. Vane-Wright of the British Museum (Natural History). He also sent photographs of an additional male specimen now in the BM which was taken recently by C. B. Roberts/BM on the Potaro River, British Guiana in 1969; it agrees completely with the type.

I took *panamensis* for the first time in February, 1968 at a hilltop in the Madden Forest Preserve. Here, with other "hill-topping" companion species of the genera *Elbella* and *Phocides*, it swept back and forth across a broad expanse of open grassy hilltop meadow with an incredibly swift and booming flight. The method for collecting was relatively simple—stand at an appropriate place in their flight pattern and, with a long-handled (about 12 feet) net, attempt to intercept them in full flight! The percentage of successful intercepts is very low, but none-the-less, rewarding.

Gordon Small's experience on many subsequent efforts in this same local reveals that *panamensis* was present very infrequently, if at all, around 11:30 A.M., and only singly. It also occasionally landed on a small bushy tree where he took all of his specimens. The *Elbella* species were also taken after alighting; *Phocides* species flew unceasing, never seeming to land.

Panamensis differs from the nominate species *zonias* in that there is no hyaline spot in space 9 on the forewing, and the width of most hyaline spots is about one-third less; the spot in inter-space 3 on the forewing is, in *panamensis*, only a fraction of the width and size of that in *zonias*. Other less obvious differences may be noted by comparing the appropriate figures.

The genitalia are identical, with the exception of the valvae; those in the nominate form are tapered rather gradually and without interruption to the terminal teeth; those of *panamensis* are

wider thru-out more of their length, finally tapering rather abruptly to the terminal teeth, particularly from the dorsal surface. The terminal teeth are somewhat blunt and there is a slight asymmetry in the valvae of both species; this latter varies slightly with each specimen thus far examined.

Zonia and its subspecies *panamensis* are both apparently very uncommon insects; I have been unable to find additional specimens in the many collections I have searched; nor have I noted its presence in the various lists that are published relevant to specific regions where it may occur. It bears a striking resemblance to *Jemadia hewitsonii albescens* Röber in size, wing shape and pattern, but a close inspection will quickly reveal the notable differences.

***Myscelus assaricus michaeli* Nicolay, new subspecies**

Figures: 1a, 1b, 2a, 2b, 8

Male: Length of forewing, 22 mm. Upperside: forewing with a yellow-orange basal area, remaining 3/4 of the wing, blue-black with an indigo sheen; a discal row of hyaline white spots in spaces 1b, 2 and across cell with the widest spot at 2½ mm in space 2; all spots clearly separated by black veins; smaller white hyaline spots in spaces 3, 4, 5 and three small rectangular apical spots in spaces 7 - 9, all forming a vague, elongate "S"-shape; a line of vaguely defined, pale blue sub-marginal spots from first apical spot in space 7 through 1b. Hindwing basal 3/4 yellow-orange, outer quarter shining blue-black with an indigo sheen; black post-discal spots from space 1b through 7, conjoined in spaces 1b to 3 and in spaces 4 and 5; an inner black spot in space 7 and inner cell, almost invisible beneath the yellow-orange overscaling; termen deeply excavate between veins 1 through 6; fringes white below vein 6. Underside: forewing dull black, white hyaline spots of the upperside repeated; two pale bluish-white dashes above cell spot in spaces 11 and 12; a row of bluish-white spots at base of costa and sub-basal in inner cell, interspace 2 and all of 1a; a row of wide, lightly scaled blue submarginal spots from apex through space 1b. Hindwing pale blue with a macular black band near base of wing; a wider sub-median and post-median band of macular fused black spots, the two joined with a black line in space 8; a vaguely defined black outer margin; abdominal fold pale blue; fringes white from vein 7 to tornus, except black at vein ends.

Female: Length of forewing, 26 mm. Upperside: forewing maculation the same as in male, wings broader, outer margin straight. Hindwing maculation the same as in the male except the dark outer margin wider, the postdiscal spots closer to its inner edge, the wing broader and more rounded.

Above, head and collar black and white striped, tegumen, tegula and thorax densely covered with long yellow-orange hairs overlapping anterior segments of abdomen; abdominal segments ringed alternately black and pale yellow; anal tuft of long, brown pale-tipped hairs: Palpi black above, pure white below, pectus pale yellow, legs black with pale scales and long hairs; abdominal segments ringed black and white. Antennae black, pale yellow inside bend of apiculus and club.

Holotype male, Madden Forest Preserve, Panama Canal Zone, 15 July 1969, G. B. Small, collector. Allotype female, same locality, 16 July 1968, G. B. Small, collector. Paratypes: 1 ♂ same locality as holotype, 20 July 1968; 1 ♂ Gatun, C. Z., 30 Jan. 1970, 1 ♂ Gatun, C. Z., 25 April 1971, G. B. Small, collector. Two specimens in the Smithsonian's National Museum collection, a male, Carillo, Costa Rica (no date) and a female, Cayuga, Guatemala, September are also included in the type series. The holotype will be deposited in the American Museum of Natural History, New York, New York. The allotype female and one paratype male remain in the author's collection, the remainder of the paratypes, with the exception of the two National Museum specimens, in the collection of Mr. G. B. Small.

The subspecies *michaeli* extends the known range of the species complex of *Myscelus assaricus* Cramer into Central America and Mexico. *Michaeli* is most similar to the nominate form in that the hyaline spots of the forewing are approximately the same size although smaller than in *assaricus* and less than half the width of those in the subspecies *mapirica* Strand. The spots of the "S"-shaped apical row are more rectangular, almost square in *michaeli*, but very narrow and linear in the nominate form and in *mapirica*. The dark spots in the disc of the hindwing are much smaller in *michaeli* than in either of the other two subspecies, being less than half the size of those in *mapirica*, and placed closer to the inner edge of the dark margin.

The pale areas of the underside of the hindwing are bright pale blue or bluish-white in *michaeli* rather than the greenish-white of the nominate form *assaricus* and are wider and more extensive in *michaeli* with the black spots and macular bands wider and heavier in both *mapirica* and *assaricus*. The male genitalia of those few specimens available for examination appear identical. This, together with the geographical separation, consistent and obvious differences in wing maculation, establishes the basis for this subspecies identity with *M. assaricus* Cramer.

This beautiful and interesting insect is named for my oldest son Michael Darrell Nicolay who dearly loved all of nature's creatures and particularly the much maligned and misunderstood reptiles.

***Aspitha leander* Boullet**

Figures 1d, 1e, 2d, 2e, 9

Yanguna leander Boullet, 1912, *Bull. Soc. Ent. France*, p. 92.*Yanguna parima* Plotz, Mabilille and Boullet, 1908, *Ann. des Sciences Nat.*, Paris, 9th Series, pp 187-88, pl 13, fig 3.*Yanguna parima* Plots, Draudt in Seitz, 1921, *Mac. Lep. of the World*, vol 5, p 842, pl 164d.*Yanguna leander* Boullet, Bell, E. L., 1933, *Hesperiidae*, *Jour. N. Y. Ent. Soc.*, vol XL1, Sept. pp 288-89.*Aspitha leander* Boullet, Evans, W. H., 1951, *A Cat. of the Am. Hesp. in the B. M. (Nat. Hist.)* Part 1, p 84.

There has been considerable past confusion regarding this species. Described by Boullet in 1912, it none-the-less was figured in color in a paper co-authored by Boullet (1908) four years earlier as *Yanguna parima* Plotz. Seitz' (1921) figure of *parima* is in reality that of *Aspitha leander* Boullet as noted by Evans (1951). Bell (1933), although he had no specimens before him, authored an excellent, brief translation of Boullet's original description of the male *leander* that fits very well the species found in Panama. *Aspitha parima* Plotz, although obviously very closely related, is a separate species found in Surinam.

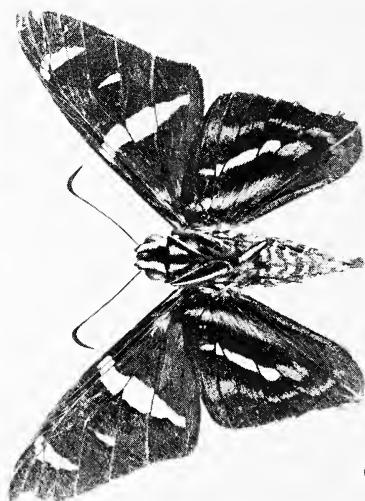
Apparently no females of *leander* had been taken or associated with the male. Evans (1951) does not mention the female, nor are characters of the female included as part of his keys. Early in 1973 Mr. G. B. Small took a pair of *A. leander* at Gatun in the Canal Zone. A description of the female follows:

Female: Length of forewing, 26 mm. Upperside: fore and hindwing color blue-black; forewing with a broad (3-4 mm) central white hyaline band from vein 1 in interspace 1b (triangular) through upper cell with a thin, broad spot in interspace 11; two tiny white hyaline spots midway between the central hyaline band and outer margin in interspace 4, the lower adjacent to vein 4, the upper, next to vein 5, a third spot above this in interspace 5; fringes whitish from vein 1 to vein 3. Hindwing with a red tornal spot 2 mm wide from inner angle through interspace 1c, with a thin, black lined outer margin, wider at end of vein 1b; fringes white from vein 1 through vein 7. Underside: all wings blue-black; markings on both wings the same as above with an additional thin line of white scales in interspace 12 above spot in interspace 11 on the forewing; wing basal area faintly paler.

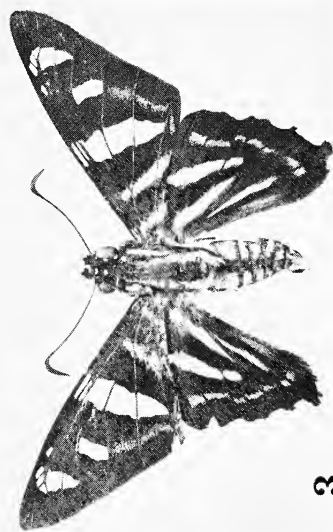
Head black with small white spots at the base of and between the antennae; tegulae black, patagia at end of tegulae red; thorax and abdomen black above and below, a few whitish hairs in anal tuft. Mid and hind legs black, forelegs black with a few white hairs on femur; palpi black, a thin line of white scales in the center; a narrow line of white scales across forehead between tips of the palpi. Antennae black.



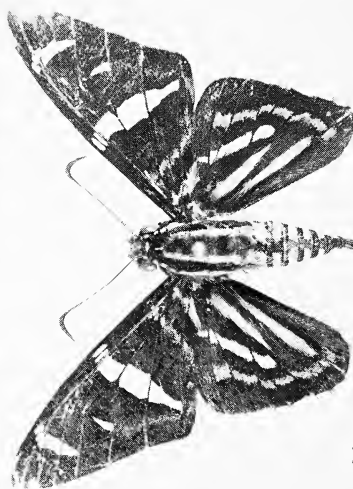
4



6



3



5

Fig. 3 and 4. — *Zonia zonias* Evans, holotype ♂, Teffe (Ega), Amazonas, M. de Mathan, 1er trimestre 1879/ R. Oberthür Coll, B. M. 1931-136, upper and underside.
 Fig. 5 and 6. — *Zonia zonias panamensis* Nicolay, holotype ♂, Madden Forest Preserve, Canal Zone, 6 February 1968, collector, S. S. Nicolay, upper and underside.

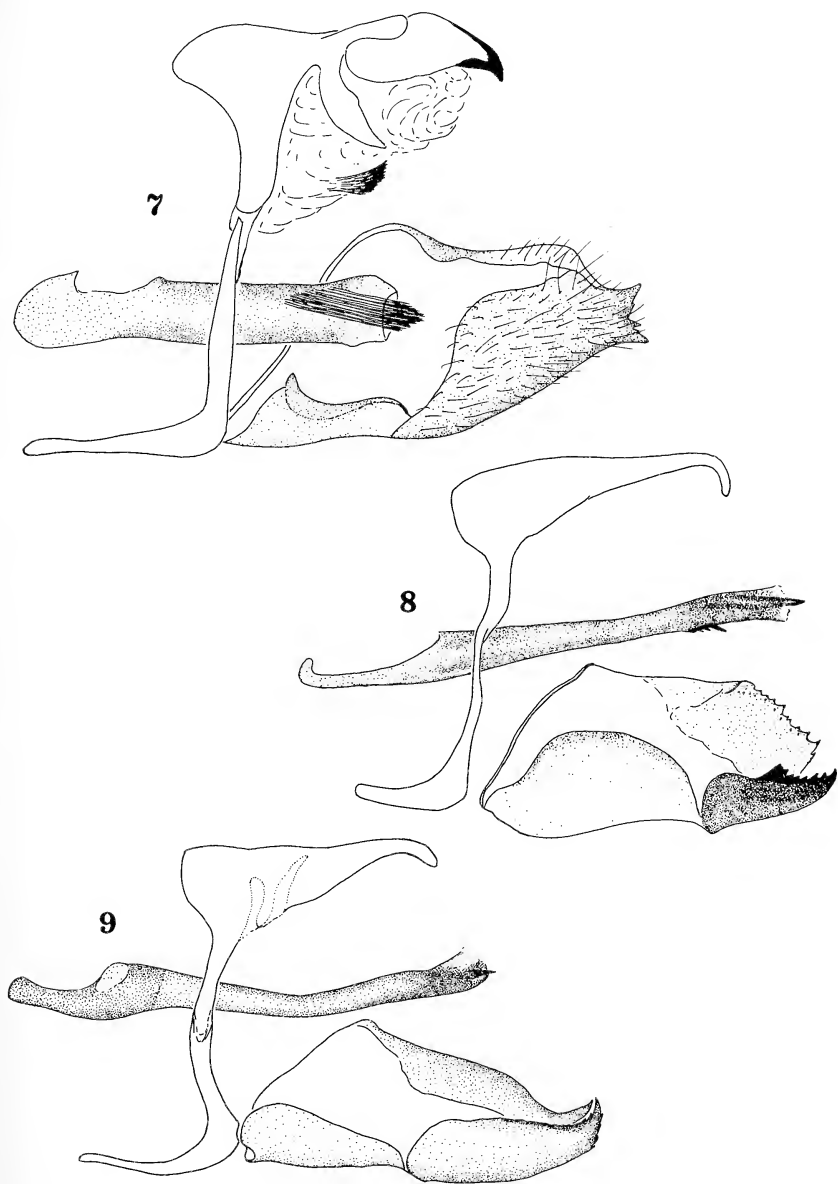


Fig. 7 - 9. — Male genitalia, reading from top to bottom (7) *Zonia sonia panamensis* Nicolay; (8) *Myrcelus assaricus michaeli* Nicolay; (9) *Aspitha leander* Boulet. All drawings with left valva removed, aedeagus in position, and inner surface of right valva detailed.

It is indeed fortunate that the two specimens figured were caught *en copula*. The sexual dimorphism apparent in this very uncommon species is great enough to make matching the sexes very difficult. In addition to the obvious differences in wing fascia, as illustrated in figures 1 and 2, the hindwing in the female is not as irregular nor as sharply produced at the tornus and at the ends of veins 1b and 2; the forewing is less sharply produced at the apex and overall, more rounded and full. Another female collected near Colon in the Republic of Panama in 1969 is without the sub-apical dots of the specimen figured and described herein, but is otherwise identical.

Aspitha leander has not been previously recorded from the Republic of Panama. The type locality is Muzo, Colombia, 800 meters.

ACKNOWLEDGMENTS

I wish to express my appreciation to Gordon B. Small, Balboa, Canal Zone for his generous logistic support of my collecting efforts and for his invaluable assistance in the field work that made this study possible. I am especially grateful to Mr. R. I. Vane-Wright on the staff of the British Museum (Natural History) for his helpful suggestions, and excellent photographs and sketches of the Evans' *zonias* type material. My thanks also to Wm. D. Field, U. S. National Museum and Dr. F. H. Rindge, American Museum of Natural History for providing the assistance and cooperation that allowed me to examine and study the collections in their care.

Photographs of the *panamensis* type were made with the help of WO G. G. Thomas, and SSgt. Richard E. Banzal of the U. S. Marine Corps. The color transparencies and line drawings were made by the author.

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BUTTERFLIES OF THE SUISUN MARSH, CALIFORNIA

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AT THE TIME OF EUROPEAN COLONIZATION, California had an estimated five million acres of wetlands. By 1973 only a tenth of that acreage remained, with a current rate of loss of one percent per year. California, unlike the eastern United States, is considered to have a depauperate marsh fauna of butterflies, and its wetlands have received very little attention from collectors.

The Suisun Marsh is a complex of tidally influenced wetland habitats covering some 44,000 acres in Solano County, west-central California, and is one of the largest marsh tracts remaining in a reasonably natural state on the entire Pacific coast. The Marsh occupies a structural basin hemmed in by hills on three sides. These hills, part of the Coast Ranges, are arid in summer and are covered with annual grassland or open oak woodland. They apparently confer sufficient isolation on the Marsh to produce several endemic taxa of plants and animals; among these the most prominent are the Suisun Shrew (*Sorex sinuosus*) and the showy Composites *Grindelia paludosa*, *Cirsium hydrophilum*, and *Aster chilensis* ssp. *lentus*. As may be seen from Figure 1, the Marsh communicates with San Francisco-San Pablo Bays to the west and the Sacramento-San Joaquin Delta to the east, and through the latter with the Central Valley of California. A biotic connection with the San Francisco Bay salt marshes is shown by the ranges of two endemic species shared by them, the Salt-Marsh Harvest Mouse (*Reithrodontomys raviventris*) and the Composite *Grindelia humilis*.

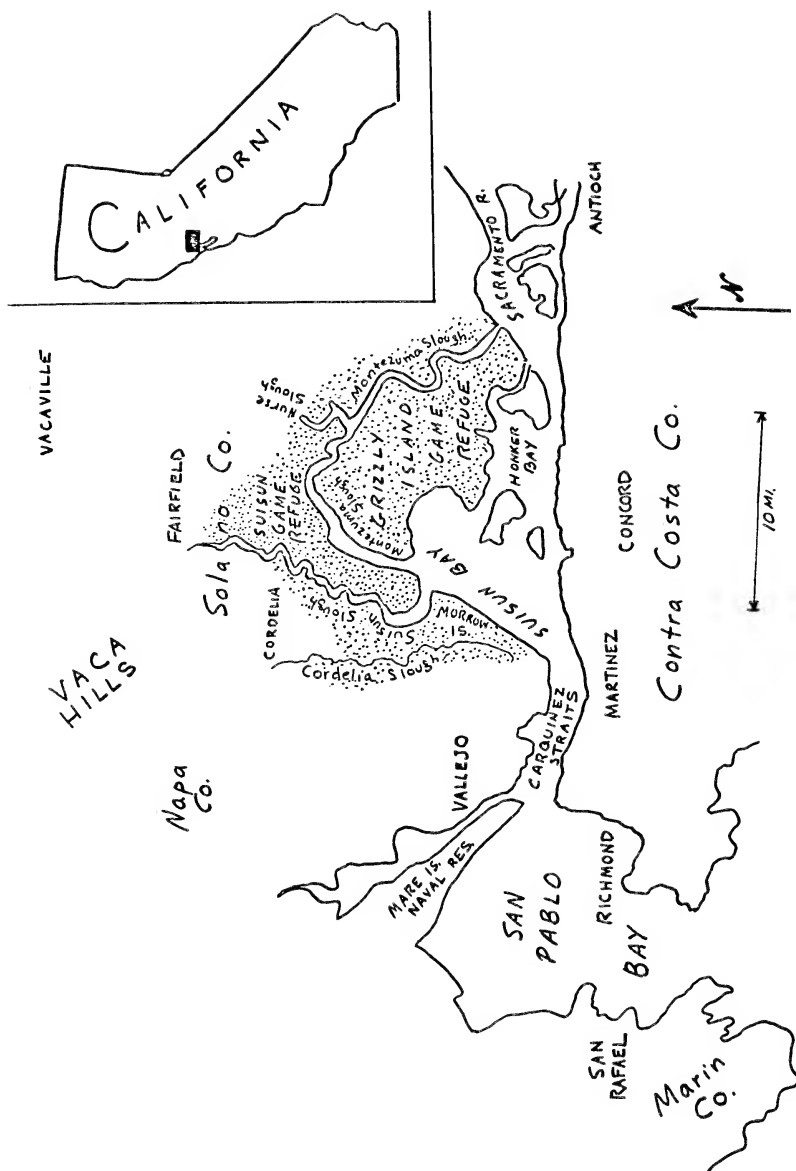


Fig. 1.—Location map of the Suisun Marsh.

CLIMATE OF THE MARSH

The Suisun Marsh differs from the Central Valley in being exposed to a stronger maritime climatic influence, which enters the basin by the Carquinez Straits. At the same time the climate of the Marsh is more continental than those of the valleys which open directly to the coast. Aside from moderating both summer and winter temperature extremes, the maritime effect increases the frequency of morning fog and low cloudiness as compared to the Central Valley, e.g. Vacaville ten miles to the east; but unlike immediate coastal sections, the Marsh very rarely has *persistent* fog or cloud in summer. More dramatically, the maritime air produces frequent sustained high winds as it rushes through the Straits to fill up the thermal low-pressure trough in the interior. Winds in excess of 20 knots probably occur on 100 days or more each year in the Marsh, blowing usually from the west ("Suisun" means "west wind" in the local Indian dialect, and is still used locally as a name for this wind).

The U.S. Weather Bureau maintains a reporting station at Fairfield. This location receives from 30-50 days with maximum temperatures greater than or equal to 90°F (32.2°C) and 15-40 days with minimum less than or equal to 32°F (0°C) per season. Temperatures in excess of 100°F (37.7°C) occur 3-5 times/season and below 30°F (-1.1°C) a similar number of times. Data for 1971 and 1972 monthly temperatures are given in Table 1. Precipitation of about 24 inches falls from October to May; there is little or no precipitation in summer. Relative humidity in summer is, however, consistently higher than in the Sacramento Valley and the Marsh is sheltered from the full force of the hot, dry "northers" which produce the most extreme summer weather in the Valley.

HABITATS OF THE MARSH

Most of the Suisun Marsh is under the control of hunt clubs whose management practices vary widely. Portions of the Marsh are cut over or burned from time to time; through an extensive system of levees, ditches, and gates the water level may be manipulated on individual parcels of land. Soil salinity is thus extremely variable from parcel to parcel. The overall result is a complex vegetational mosaic which for convenience may be divided into "high marsh," "low marsh," and "landfill."

Table 1. Temperature data in °F for Fairfield Fire Station, California, 1971-72.

Month	1971				1972*					
	Mean T, °F max.	min.	Monthly extremes highest lowest	days >90°F	days ≤32°F	Mean T, °F max.	min.	Monthly extremes highest lowest	days >90°F	days ≤32°F
J	55.0	38.0	65 26	0	7	49.6	32.7	56 24	0	18
F	60.5	38.1	70 31	0	2	60.9	41.0	71 31	0	3
M	64.4	42.8	77 29	0	3	70.4	44.5	82 34	0	0
A	68.1	43.7	79 38	0	0	69.2	44.4	80 37	0	0
M	72.0	48.2	82 36	0	0	79.1	48.5	95 43	4	0
J	82.2	53.1	97 43	5	0	85.1	52.1	103 44	8	0
J	88.2	55.5	99 50	11	0	84.6	56.3	108 51	9	0
A	90.2	57.4	106 51	17	0	87.7	56.7	99 49	12	0
S	87.4	54.0	107 43	15	0	82.0	53.8	90 46	1	0
O	75.5	45.0	91 37	2	0	71.7	51.3	88 38	0	0
N	64.0	40.2	76 33	0	0	59.6	42.8	68 32	0	1
D	51.9	34.9	63 27	0	11	49.9	34.5	68 19	0	13
Totals: 50				23	Totals: 34				35	

*Although 1972 was a "cool" year, a brief period of record-breaking heat occurred in July.

"High Marsh" — This group of associations occurs in areas of low salinity: high points (islands) within the Marsh, levees and the edges of sloughs, ditched marshland and fresh-water pools. It has the highest plant species diversity in the Marsh, and is characterized by the aspect dominance of showy Composites in late summer. Some characteristic plant species are: *Grindelia humilis*, *G. paludosa*, *Aster chilensis* ssp. *lentus*, *Baccharis douglasii*, *Cirsium hydrophilum*, *Solidago occidentalis*, *Achillea borealis* ssp. *arenicola*, *Pluchea purpurascens*, *Cicuta bolanderi*, *Apium graveolens*, *Potentilla egedei*, *Atriplex patula* var. *hastata*, *Phragmites communis* var. *berlandieri*, *Scirpus olneyi*, *S. koilolepis*, *S. acutus*, *Juncus effusus* var. *brunneus*, and *Typha latifolia*.

"Low Marsh" — This association, or group of associations, covers the most extensive part of the Marsh. It occupies areas of high salinity which are saturated or shallowly inundated at high tide. The dominant plants throughout are *Distichlis spicata* and *Salicornia virginica*. Characteristic associates are: *Atriplex patula* var. *hastata*, *Lilaeopsis occidentalis*, *Polygonum aviculare* var. *littorale*, *P. fowleri*, *Cotula coronopifolia*, *Frankenia grandifolia*, *Eryngium articulatum*, *Rumex crispus*, *Juncus acutus* var. *sphaerocarpus*, *J. bufonius*, and *Scirpus olneyi*.

"Landfill" — In many places marshland has been filled in with construction debris or other refuse, or with clay soils from the uplands. Plants found in such sites are typical weeds of highly disturbed lowland sites in California: *Centaurea solstitialis*, *Cichorium intybus*, *Lactuca serriola*, *Cirsium lanceolatum*, *Silybum marianum*, *Malva rotundifolia*, *M. nicaeensis*, *Sida hederacea*, *Convolvulus arvensis*, *Epilobium paniculatum*, *Atriplex rosea*, *A. semibaccata*, *Polygonum aviculare*, *Foeniculum vulgare*, *Bromus rubens*, *B. rigidus*, *Avena barbata*, etc. The transition from marsh to annual weeds occurs at about four feet above sea level, the mean highwater mark at Suisun. *Baccharis pilularis* ssp. *consanguinea* and *Tamarix pentandra* form thickets just above this level.

THE BUTTERFLY FAUNA

So far as I have been able to determine, the Suisun Marsh has never been collected systematically for butterflies before 1972. In 1972 and 1973 I visited it at frequent (usually 2-4 weeks) intervals and recorded all butterfly species present. The seasonal distributions of the 40 species recorded are given in Figures 2 and 3. It is likely that one more resident and five to

ten immigrant or stray species (from the hills) may be found in the Marsh. All of the resident species recorded in the Marsh occur in both the San Francisco Bay area and the Central Valley (except *Ochlodes yuma*, unrecorded from the Bay but to be expected). Two endemic populations of widespread species occur in the Suisun Marsh. They are the *Potentilla*-feeding strain of *Lycaena helloides* and the large, richly colored *Phyciodes campestris* associated with *Aster chilensis* ssp. *lentus*. Both have been sought, but not yet found, in salt marshes around the Bay area and in Marin County. They are discussed individually, below.

SYSTEMATIC LIST

Danaus plexippus (L.) — Occasional to frequent, especially in autumn; throughout. Larvae on *Asclepias fascicularis* on landfill. Does not overwinter at Suisun.

Coenonympha tullia californica West. — Rare stray from the hills; not known to breed in the Marsh. Is striking that the *C. tullia* complex has not evolved salt-marsh populations on the Pacific Coast as it has elsewhere in its vast range.

Speyeria coronis (Behr). — One female, certainly a stray from the hills. No violets are recorded in the Marsh, but *Viola pedunculata* occurs in the Potrero Hills and on Mt. Diablo.

Euphydryas chalcedona (Dblly). — One male, a stray from the hills.

Phyciodes mylitta (Edw.).—Frequent on levees and high marsh; multiple-brooded. Larvae common on *Silybum* on landfill, but not yet found on *Cirsium hydrophilum*.

Phyciodes campestris (Behr). — Unaccountably rare. The 7 Marsh specimens are phenotypically very distinct from the usual lowland *P. campestris* (Fig. 4), particularly in the lack of contrast between the median spot-band and the ground color; the very well-developed submarginal spot-band; the reduced amount of black above; and the larger size. They were taken on flowers of *Aster chilensis* ssp. *lentus* and may represent an endemic population developed in association with this plant, but until more information and specimens become available it seems best to defer naming them.

	vi.25	vii.16	vii.23	viii.25	ix.23	x.21	xi.5
<i>D. plexippus</i>			X	X	X	X	
<i>C. t. californica</i>							
<i>S. coronis</i>					X		
<i>E. chalcedona</i>							
<i>P. mylitta</i>		X	X		X		
<i>P. campestris</i>							
<i>N. antiopa</i>	X						
<i>N. californica</i>							
<i>V. atalanta</i>							
<i>C. virginicensis</i>						X	
<i>C. carye</i>	X	X	X	X	X	X	X
<i>C. cardui</i>					X		
<i>P. coenia</i>	X	X	X	X	X	X	X
<i>L. lorquini</i>							
<i>L. bredowii</i>							
<i>S. melinus</i>	X	X	X	X	X	X	
<i>S. sylvinus</i>							
<i>S. californica</i>							
<i>L. helloides</i>	X	X	X	X	X	X	X
<i>L. xanthoides</i>	X	X					
<i>B. exilis</i>	X	X	X	X	X	X	X
<i>E. comyntas</i>	X		X				
<i>P. acmon</i>	X	X	X	X	X		
<i>E. ausonides</i>							
<i>C. eurytheme</i>	X	X	X	X	X	X	X
<i>P. rapae</i>	X	X	X	X	X	X	
<i>P. protodice</i>							
<i>B. philenor</i>							
<i>P. zelicaon</i>		X		X	X	X	X
<i>P. rutulus</i>							
<i>E. tristis</i>				X			
<i>P. communis</i>	X	X	X	X	X	X	X
<i>P. scriptura</i>		X	X	X	X		
<i>P. catullus</i>	X	X	X	X	X	X	X
<i>H. phylaeus</i>	X	X	X	X			X
<i>A. campestris</i>		X	X				
<i>P. sabuleti</i>	X	X	X	X	X	X	X
<i>O. sylvanoides</i>			X	X	X		
<i>O. yuma</i>	X		X				
<i>L. eufala</i>		X		X	X	X	X
Total species:	16	18	19	18	19	14	11

Fig. 2.—Seasonal distribution of butterflies at Suisun, 1972.

	7	11	10	13	23	19	22	18	19	16	23	26	21	21	9	8	8	X
B. exilis						X	X	X	X	X	X	X	X	X	X	X	X	X
E. comyntas		X			X	X	X	X					X					X
P. acmon					X	X	X	X	X	X	X	X	X	X				
E. ausonides	X	X	X	X	X													
C. eurytheme	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
P. rapae	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
P. protodice																		
B. philenor					X													X
P. selicaon	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	
P. rutulus	X		X		X			X	X									
E. tristis		X			X						X							
P. communis			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
P. scriptura		X			X	X	X	X	X	X	X	X	X	X				
P. catullus		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
H. phylaeus						X		X			X	X	X	X	X	X	X	X
A. campestris			X								X	X	X	X				
P. sabuleti		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
O. sylvanoides							X	X	X	X	X	X						
O. yuma											X							
L. eufala											X	X	X	X				
Total species:	7	11	10	13	23	19	22	18	19	16	23	26	21	21	9	8	8	7

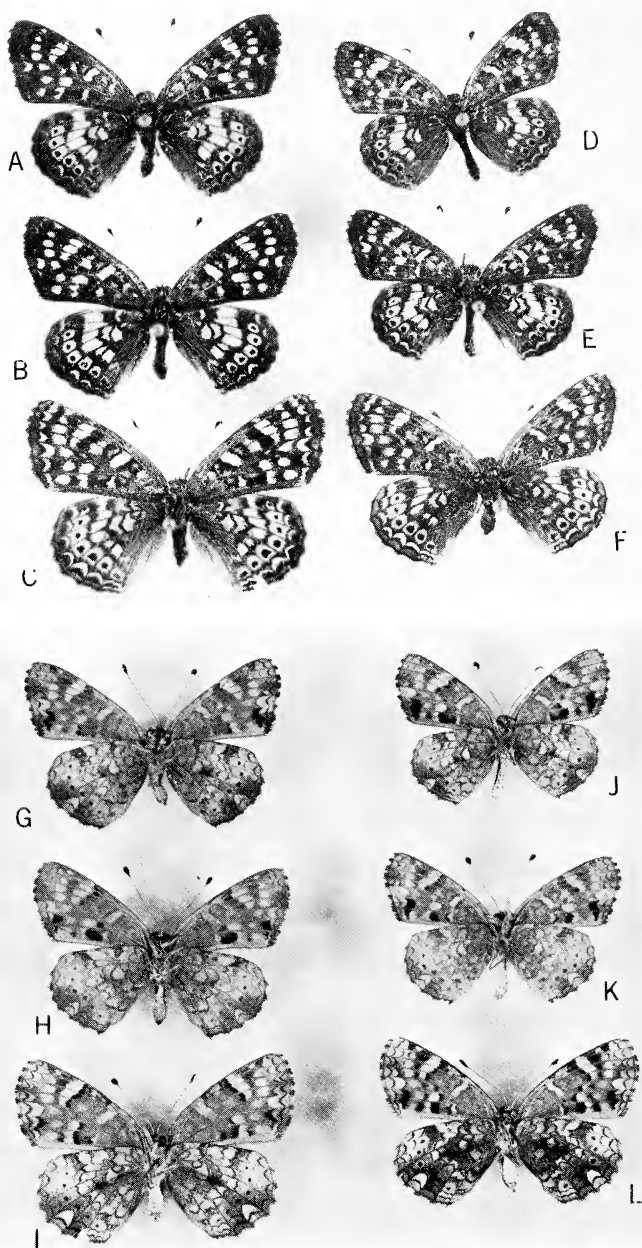


Fig. 4.—*Phyciodes campestris* from lowland central California. a-c, g-i, Suisun Marsh, X.12.73; d-f, j-l, Willow Slough, Yolo Co., X.19.73.

Nymphalis antiopa (L.) — Occasional throughout. Larvae occasionally abundant on *Salix lasiandra* along ditches.

Nymphalis californica (Bdv.).—Occasional as a migrant through the Marsh, but not breeding; no *Ceanothus* occur in the basin. *Vanessa atalanta* (L.). — Occasional throughout, mostly in high marsh; multiple-brooded. Larvae on *Urtica holosericea* (Joice Island).

Cynthia virginiensis (Drury). — Occasional throughout; the least common *Cynthia*, but still commoner than in most of the Sacramento Valley. Larvae on *Gnaphalium bicolor* (Joice Island; levees near Suisun City).

Cynthia carye Hbn. (= *annabella* Field).—Common everywhere; multiple-brooded. Larvae common on *Malva rotundifolia*, *M. nicaeensis*, *Althaea rosea*, and *Sida hederacea* (all Malvaceae) on landfill. A striking aberration was taken in the Marsh, v.19.73, figured in Shapiro, 1973.

Cynthia cardui (L.). — Common throughout. Does not appear to overwinter. Larvae on *Silybum marianum*, *Cirsium lanceolatum*, *Centaurea solstitialis*, *Malva* spp., and *Amsinckia douglasiana* on landfill; on *Cirsium hydrophilum* on high marsh.

Precis coenia (Hbn.). — Common to abundant everywhere, especially in late summer and autumn; September-October specimens are often very red beneath. Larvae on *Plantago coronopus* in low marsh, *P. lanceolata* and *Lippia nodiflora* on landfill.

Limenitis lorquini (Bdv.). — Occasional along sloughs near willows, probably breeding.

Limenitis bredowii californica (Butl.). — Recorded once; stray from foothills.

Strymon melinus Hbn. — Frequent to common throughout, all season.

Satyrrium sylvinus (Bdv.). — Locally frequent in clumps of *Salix hindsiana* along ditches, otherwise not seen.

Satyrrium californica (Edw.). — One male, in high marsh on celery blossoms, certainly a stray from the hills.

Lycaena helloides (Bdv.). — Abundant. On landfill associated with *Polygonum aviculare* and *Rumex crispus*; in high marsh, especially deep in the Marsh, with *Potentilla egedei*. The two strains are slightly differentiated phenotypically in a statistical sense, and are not altogether synchronized in brood sequence. See Shapiro, 1974 for a fuller discussion. A bilateral gynandro-

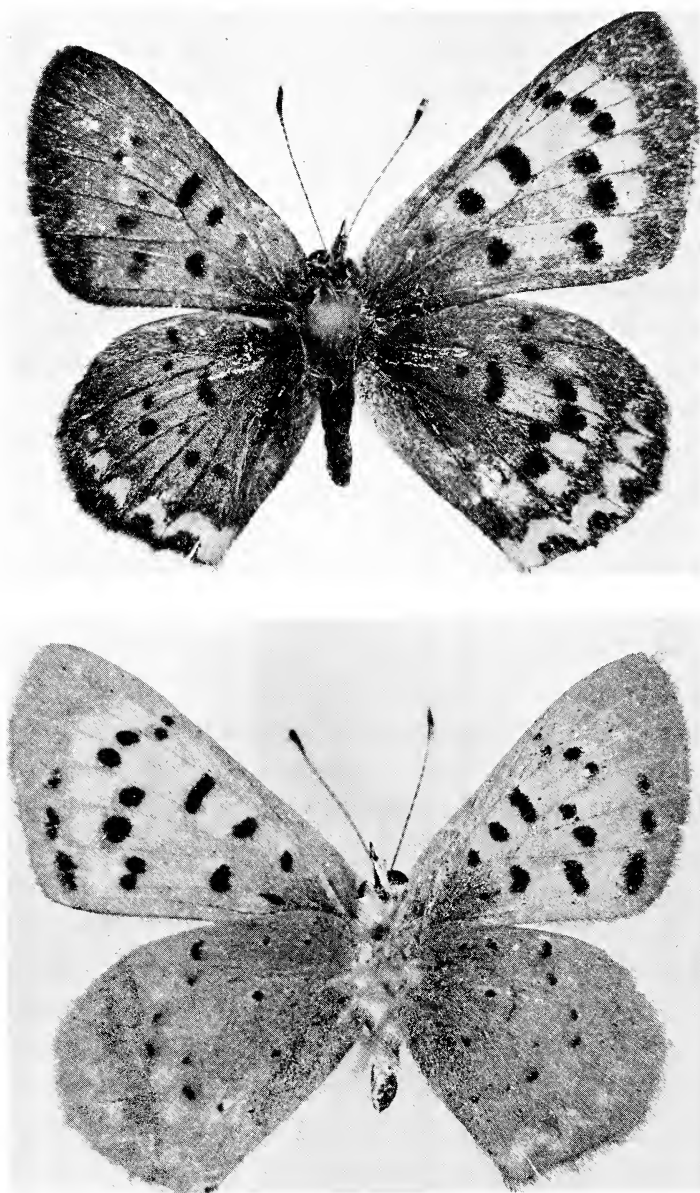


Fig. 5.—Bilateral gynandromorph of *Lycaena helloides*, Suisun, X.12.73.

morph of the *Potentilla* strain taken in high marsh, X.12.73 is shown in Figure 5.

Lycaena xanthoides (Bdv.). — Abundant on landfill and low marsh, associated with *Rumex crispus*; one brood. Suisun specimens average smaller and duller in color than Central Valley ones, and show some local differentiation.

Brephidium exilis (Bdv.). — Scarce early in the season, but becoming very abundant in September-October. Throughout, commonest on low marsh and landfill. Larvae abundant on *Atriplex patula* var. *hastata*, *A. rosea*, and *A. semibaccata*.

Everes comyntas (God.). — Locally frequent along ditches; occasional in high marsh; in spring common on landfill. Larvae on *Lotus purshianus*, *L. strigosus*, and *Vicia sativa*.

Plebeius acmon (West. & Hew.). — Common throughout. Spring and fall males, and spring females of f. vern. "*cottlei*". Larvae on *Polygonum aviculare* on landfill.

Euchloe ausonides Lucas. — Frequent to locally common on landfill; occasional on high marsh. Two broods. Larvae on *Raphanus sativus* and *Brassica nigra*.

Colias eurytheme Bdv. — Common everywhere, especially in September and October. Larva on *Vicia sativa* on landfill—doubtless on a wide variety of legumes as elsewhere.

Pieris rapae (L.) — Common throughout. Larvae on *Brassica nigra* and *B. arvensis* and *Raphanus sativus* on landfill.

Pieris protodice Bdv. & LeC. — Occasional on landfill near Suisun City, in annual grassland; strays into marsh.

Battus philenor hirsuta (Skinner). — Occasional stray from nearby canyons; once fresh in Suisun City, xii.3.73.

Larvae abundant on *Foeniculum vulgare* on landfill and levees. *Papilio zelicaon* Lucas. — Abundant on high marsh and landfill. Not recorded on *Cicuta* or *Apium* in high marsh, although both are acceptable in the laboratory.

Papilio rutulus Lucas. — Occasional in high marsh; not known to breed, but suspected of doing so on cottonwoods or willows, as on Joice Island.

Erynnis tristis (Bdv.). — Infrequent on landfill and on high marsh; presumably a stray from the hills.

Pyrgus communis (Grote). — Abundant on landfill; occasional on high marsh; all season. Larvae common on *Malva rotundifolia*, *M. nicaeensis*, and (occasionally) *Sida hederacea*.

Pyrgus scriptura (Bdv.). — Abundant on landfill near the host plant, *Sida hederacea*.



Fig. 6.—Variation in male *Polites sabuleti*. a-c, e-g, Suisun Marsh, X.12.73. d, h, *P. s. tecumseh*, Donner Pass, Placer Co., el. 6975', viii.17.73.

Pholisora catullus (Fabr.). — Common on landfill; occasional on low marsh. Larvae on *Amaranthus hybridus* on landfill.

Hylephila phylaeus (Drury). — Common throughout, especially in September and October.

Atalopedes campestris (Bdv.). — Frequent on landfill; occasional elsewhere.

Polites sabuleti (Bdv.). — Very abundant on low marsh and landfill. Extremely variable; a few specimens (cf. Fig. 6) indistinguishable from *P. s. tecumseh* of the high Sierras. Larvae common on *Distichlis spicata*.

Ochlodes sylvanoides (Bdv.). — Common throughout; at least two broods.

Ochlodes yuma (Edw.). — Locally frequent around stands of *Phragmites*, as at the Suisun City marina and along Highway 21 north of the Fairfield City Limit. Two broods.

Lerodea eufala (Edw.). — Frequent in all habitats in late summer and autumn. Larvae on *Sorghum halepense*, *Echinochloa crus-galli*, and *Cynodon dactylon* on landfill and along ditches.

DISCUSSION

There is surprisingly little phenological difference in the butterflies of the Suisun Marsh and the Central Valley. The only conspicuous example is *Papilio zelicaon*, which flies into mid-November at Suisun 6-8 weeks after it has disappeared in the Valley. It is also more abundant at Suisun than in the Valley. *Brephidium exilis*, which is largely a species of saline and alkaline situations, is near its northern limit in both areas and may not always overwinter. In 1972 it flew earlier at Suisun than in the Valley, but in 1973 the situation was reversed. Flight activity at Suisun is limited by wind probably to about the same degree as it is prevented by heat and dryness in summer in the Valley. In most of California the maximum numbers of individuals and species fly in spring or early summer; at Suisun this peak occurs in September and October.

The Suisun Marsh receives no summer rain, but its year-round water supply and the halophytic habit of many of its plants provide a constant supply of butterfly host plants and nectar sources. In most of lowland California there is a summer die-off of annuals; most such places have a fauna including many vernal univoltine species. In the nearby Vaca hills in Yolo and Solano Counties 25 of 65 recorded taxa are univoltine (39%), for example. In the Sacramento Valley the moist riparian habitats

and agricultural irrigation allow for a much more multivoltine fauna (8 of 47 breeding taxa are univoltine, 17%). The Suisun Marsh has the most strongly multivoltine fauna recorded in California—only 2 of 33 breeding taxa are univoltine (*Satyrium sylvinus*, *Lycaena xanthoides*), or 6%. (Of the 6 immigrant taxa from the hills, however, 3 are univoltine—*S. coronis*, *E. chalcidona*, *S. californica*.) Except for *Euchloe ausonides*, *Lerodea eufala* and the two *Ochlodes*, the remaining species are apparently continuously brooded all season. The brood sequence of *Phyciodes campestris* is unknown.

Only one additional resident species, *Polygonia satyrus* (Edw.) is likely to be found. Its host, *Urtica holosericea*, is locally common in the Marsh. Almost any common foothill species, and some of the less common ones, may turn up eventually in the Marsh. There is a remote possibility that *Cercyonis pegala ariane* (Bdv.) may turn up somewhere in the Marsh; it is unrecorded in Solano County but is found only 15 miles away in Contra Costa County in similar habitats.

The Suisun butterfly fauna contains a large proportion of weedy or adventive species. This is the case with most of lowland California. Although locally differentiated populations of two species occur at Suisun, the lack of butterflies and skippers associated with the many distinctive plants—especially grasses and sedges—is as striking there as elsewhere. The reclamation of marshland in the Central Valley may have destroyed some endemic Lepidoptera, but the absence of relict populations from places as little disturbed as parts of the Suisun Marsh argues for a genuine lack of wetland species in California.

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THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

CONTENTS

Volume 11 Number 1 March, 1972

THE BUTTERFLIES OF NEBRASKA

KURT JOHNSON

Volume 11 Number 2 June, 1972

- The Neotropical Nymphalid Butterfly,
Anartia amathea Michael K. Fosdick 65
- On the distribution of
some Skippers in Ontario J. C. E. Riotte 81
- Observations on life history of
Oarisma powesheik (Parker) 1870
Wilbur S. McAlpine 83
- Habitat: *Oeneis jutta ascerta*
Masters & Sorensen John H. Masters 94
- Dispersal in a cosmopolitan
butterfly species (*Pieris rapae*)
having open population structure
Thomas C. Emmel 95
- Mating of Butterflies James A. Scott 99
- Book Review ---
Butterflies of Georgia F. A. Urquhart 128

Volume 11 Number 3 September, 1972

IN THIS ISSUE

- Gynandromorphism in *Pieris brassicae* L.
Brian O. C. Gardiner 129
- Two new subspecies of *Euphydryas*
chalcedona from the Mojave desert of
Southern California T. C. Emmel and J. F. Emmel 141
- Butterflies of middle and southern
Baja California Richard Holland 147
- Vital staining as evidence for wing
circulation in the cabbage butterfly
Pieris rapae John M. Kolyer 161

A dwarf form of <i>Euptoieta claudia</i>	Russell A. Rahn	174
Butterfly records for three northwest Wisconsin counties	John H. Masters	152
Variations of <i>Parasemia parthenos</i>	A. E. Brower	183
A search for <i>Speyeria nokomis coerulescens</i> (Holland) (Nymphalidae) in southern Arizona	Ronald S. Wielgus	187
A bilateral gynandromorph of <i>Limenitis weidemeyerii latifascia</i> (Nymphalidae)	E. M. Perkins and T. F. Perkins	195
An interfamilial courtship (Nymphalidae, Pieridae)	Arthur M. Shapiro	197
Addition to : "A checklist of Utah butterflies and skippers"	Curtis J. Callaghan and Norman B. Tidwell	199

Volume 11 Number 4 December, 1972(1973)

IN THIS ISSUE

Latitudinal gradients in species diversity of the new world swallowtail butterflies	Frank Slansky, Jr.	201
Lack of melanism in <i>Colias</i>	John H. Masters	218
A population study of <i>Euptychia hermes</i> in northern Florida	Thomas S. Kilduff	219
<i>Limenitis weidemeyerii angustifascia</i> X <i>L. astyanax arizonensis</i> = (?) ab. <i>doudoroffi</i> (Gunder) 1934.	E. M. Perkins, Jr. and John S. Garth	229
A new subspecies of <i>Gonepteryx amintha</i> (Pieridae) from Yunnan, mainland China.	Yuri P. Nekrutenko	235
Reduction of abdominal scales of the Monarch butterfly imago as a result of cauterizing the Abd PPM of the pupa.	F. A. Urquhart	241
Some techniques for the rearing of <i>Megathymus</i> larvae	Ronald S. and Dale Wielgus	245
Concerning <i>Heliconius cydno</i> aberration "larseni" Niepelt	John H. Masters	251
Polymorphism in two species of Alaskan <i>Boloria</i>	C. D. Ferris	255
A new species of <i>Nephelodes</i> Guenee from the Great Basin	John S. Buckett	260

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THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

Volume 13

Number 3

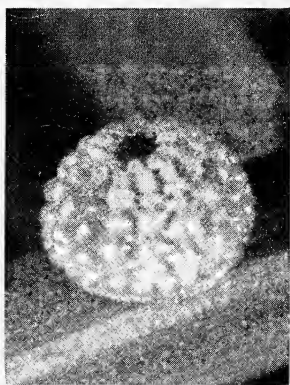
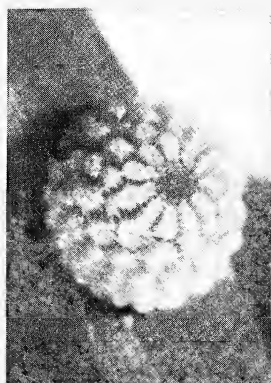
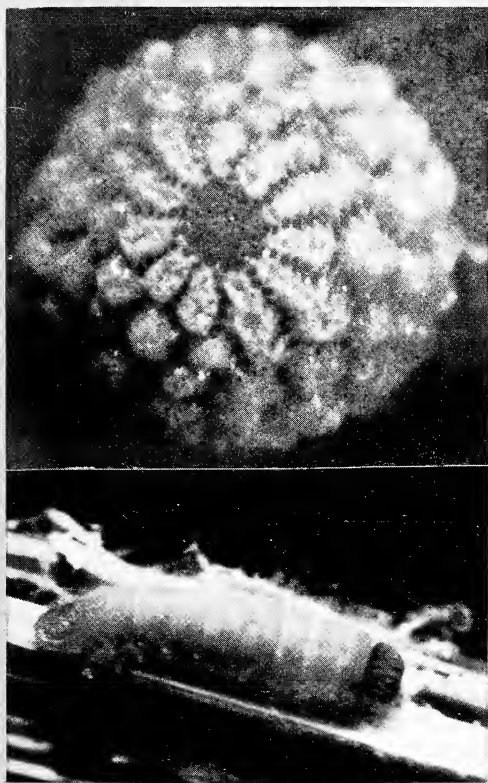
September, 1974

IN THIS ISSUE

- Studies of the ova and first instar
larvae of Geometridae (Ennominae). I.
Roger L. Heitzman 149
- Altitudinal migration of central California butterflies
Arthur M. Shapiro 157
- The chromosomes of *Apantesis phalerata*,
A. radians, and their hybrid in Florida populations
(Arctiidae) Jack S. Bacheler and
Thomas C. Emmel 162
- A partial bibliography of the world distribution
and zoogeography of butterflies
Oakley Shields 169
- The nomenclature in an important British checklist (1972)
Part 2: Corrections of family-group names for
Geometridae (Lepidoptera) Juraj Paclt 179
- Illustrations and descriptions of
species of some Pyrrhopyginae from Panama
(Hesperiidae) S. S. Nicolay 181
- Butterflies of the Suisun Marsh, California
Arthur M. Shapiro 191

THE JOURNAL
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TOWARD A THEORY OF BUTTERFLY MIGRATION

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INTRODUCTION

IT IS DIFFICULT TO KNOW what observations are important or critical in explaining why and how butterflies migrate, but since so many have been made, some of these are bound to be of significance. Regrettably, there is a nearly total lack of experimental work. A good working model is sorely needed; the lack of this has no doubt severely hampered progress in this field. This report is my attempt to extract a working hypothesis from the morass of published data.

Butterfly migrations can reach spectacular proportions. In 1926 in East Africa about 36 million *Belenois mesentina* crossed each mile of front per day, and in 1924 in southern California about 3 billion *Vanessa cardui* crossed a 40-mile front (Williams, 1949)! On the other hand, flights may be "so thin that each butterfly may be hundreds of yards from its nearest companion," out of sight of each other (Williams, 1949).

The two questions which most commonly occur are: (1) Why do they migrate?, and (2) What determines the direction of migration? (Abbott, 1950).

Various authors have offered their definition of butterfly migration. (Poulton, 1902, says that *emigration* is a better term than migration, for masses of insects moving out of an overcrowded area, but the term does not specify that a unidirectional flight also occurs.) Wiltshire (1946) says as a general rule, migrant Lepidoptera do not perform a diapause. "A species can be considered a migrant if it fulfills most or all of the following provisions:—(1) it has been observed performing a mass movement; (2) it has been taken, or seen on the wing, at sea; (3) it shows no geographical variation over a wide and diverse area; (4) both sexes occur occasionally, or sporadically, far from where it is known to breed and reside." "A migration is recognized

when the butterflies, whether few or many, are all at the same time flying in the same direction, as if guided by a compass" (Abbott, 1951). Williams (1957) says that insect migration refers "to movements of animals in a direction and for a distance over which they have control, and which result in a temporary or permanent change of habitat." "Migration is a persistent, straightened-out movement with some internal inhibition of the responses that will eventually arrest it" (Kennedy, 1961). Johnson (1960) says that insect migration is so variable that definitions based on what is or is not migration or what is active migration and passive dispersal become arbitrary and unsatisfactory when applied to all migratory insects.

EXAMPLES

Details of five species of migrants are presented below which are well-known in the literature, in hopes of revealing underlying causes.

VANESSA CARDUI

Williams (1925) says that *V. cardui* in Europe in the late spring fly mostly NW. These flights come from North Africa and Asia Minor, although not from the countries immediately surrounding the Mediterranean (probably from the deserts to the south). "The movement appears to continue for many weeks or even months at irregular intervals." He says there is no evidence of a return flight in this region in autumn. It cannot overwinter in the north in any stage. "So far as we can see, all those butterflies which fly to the north of the area in which they can breed throughout the year are lost completely to the species, as either they or their offspring perish during the winter." Migrant individuals have large fat body reserves and undeveloped internal sex organs.

Abbott (1950) records that 1924 was a great migration year for *V. cardui* in southern California, while in 1925 only 2 were seen the entire spring. 1926 was another migration year, though not in such large numbers as 1924. (Thus perhaps 1925 was a population crash.) "To maintain their straight path of migration, butterflies regularly rose over obstacles such as hedges and trees, even tall eucalyptus trees and three story buildings, yet they consistently kept within a few feet of the ground otherwise." The beginning of the daily flight was noted at 6:50 am on April 25, 1941, when 6 *V. cardui* which apparently had been

"sleeping" on the lawn flew up, circled around more or less, and flew off to the northwest. (Similarly, migrant *V. cardui* I released in a room lighted by a ceiling light flew up to the light in a spiral flight, at night.) Abbott (1951) notes that in 1941 there were three waves: March 9-March 28, April 4-7, and April 15-22. In 1945 waves occurred on March 19-21, March 24-25, and March 27-29. "The same territory is covered in every migration, the extent varying with the total numbers." Flights are from February to April, averaging just under 2 months in extent. Migrations occur during years of vegetation abundance, though significantly not every "wildflower year" is a migration year. Southern California migration years were 1924, 1926, 1941, 1945, 1949. Tilden (1962) noted *V. cardui* moving NNE on May 18-19, 1958, in Oregon, and on May 20-21, moving SSW, perhaps due to meeting a cold front. He saw one *V. cardui* migration in light to heavy rain, and rather cold, though he thinks it unlikely the flight was initiated in the rain. Sampling of 2 flights by Thorne and Sette, and Tilden, yielded a 50-50 sex ratio. Tilden thinks *V. cardui* must reproduce along the line of flight.

On April 15-20, 1973, I encountered *V. cardui* migrating NNW (even against a wind) in vast numbers on the Eastern Mojave Desert, E of Ludlow 20-40 mi., by the thousands. The desert was carpeted with wildflowers. Desert blooms hit by the larvae included *Amsinkia*, *Lupinus*, *Salvia*, *Phacelia campanularia*, every Boraginaceae, and even 2 larvae on a crucifer. *V. cardui* was noted migrating and feeding in the pm and avidly feeding in the early am on white flowers in washes.

ASCIA MONUSTE

Hayward (1953) saw a migration of *A. monuste* in Argentina during the spring and summer of 1951-52. "On fine mornings the overnight ground population began to move with the first sign of daylight," seeking flowers and puddles. "Although the butterflies sometimes commenced their migratory flight directly from the flowers on which they were feeding, it was more usual for them to circle and drift upwards till they had attained certain height and there assemble before moving off." The migrations flew in various directions: 9 am = SSE then veering E; 11:30 = N (WSW wind). On December 3rd there was a massive migration that began to lessen at c. 3000', with individuals seen by airplane pilots as high as 5000'! On December 7th at 9:15 am one flight at ground level was going E, while a high-

flying swarm that was earlier going E was flying N! On January 7th the flight continued until darkness. On January 14, there was heavy overcast and no migration was observed. In one migration on October 28th, 300 specimens were taken at light on a moonless night. Females were observed laying eggs during one flight. "*Ascia monuste* on migration flies close to the ground when the wind is adverse and high when the wind is favorable. There is a tendency to fly low on cloudy days and higher in bright sunshine. The migratory swarms may reach an altitude of over 3000 ft., and mountain ranges of up to at least 5000 ft. in height do not cause the migrants to deviate from their course."

Nielsen & Nielsen (1950) report a migration of *A. monuste* at Fort Pierce, Florida, was at a maximum on April 15, and the maximum of the next outbreak was May 20, some 36 days later. They observed that a mass outbreak was necessary for a migration ("a simultaneous hatching of a whole population within a few days"). *A. monuste* migrates "*en masse* while there seems still to be ample food on which they could continue to breed in the habitat" (Johnson, 1969, p. 224).

URANIA MOTHS

Smith (1972) notes of *Urania* moths in the Neotropics, that, "Aside from the periods of population explosion and migration, the distribution of *Urania* moths over the vast area is rather localized," in low densities. "The migration is to the south and east in the autumn and westward and northward in the spring." Movement is basically east-west. The eastward movements (July-October) involve far more individuals than do the westward ones. "The most frequent interval between large flights appears to be 8 years, but there are numerous exceptions." In general there is no "return spring flight" in years following a large eastward movement in the autumn. Migrants fly all day long. Larvae eat the vine *Omphalea* (Euphorbiaceae). Some flight had many gravid females, others did not. In 1969, in the second and third weeks the frequency of gravid females increased. Copulation was rarely observed; no oviposition was observed during a flight. Release from selection pressure of predators and parasites combined with food abundance "must be responsible for the really major population explosions that have occurred." Generally when an eruption of *Urania fulgens* occurred in Central America, a simultaneous eruption occurred in *U. leilus* in South America.

DANAUS PLEXIPPUS

Tilden (1962) says that the monarch has a true migration, involving "a going out and a return," i.e. a cyclic movement. The migrants, however, do not fly in mass (Heape, 1931, p. 151). Migratory flights of monarchs end in aggregations for hibernation and thus differ from other migrant species where the flights lead to dispersal. In autumn, monarchs migrate south in the U.S. (Canada and northern U.S.), to southern California, Florida, Mexico, and hibernate gregariously in trees. They breed and migrate (disperse) north the following spring. Their foodplants grow in exposed and often semi-arid areas. Adults depart from the cold. To survive *in situ* as adult diapause in winter would be fatal. There are one to three generations in the north before next autumn. Flights are up to 1500 miles (tagged specimens). Urquhart (1960, p. 296) notes that "recovery lines" for tagged monarchs in eastern U.S. indicate a general SW flight in the fall. Spring migration records in California for tagged monarchs show a general NE or NNE trend (fig. 79, p. 320). Monarchs do seem to be affected by landmarks, water bodies, etc. in their migration flights.

Funk (1968) found *D. plexippus* in December at Yuma, Arizona, as ova, larvae, pupae, and adults. The implication is that a return flight might be from this new brood rather than from overwintering adults. (Marked specimens could not be recaptured in the area.)

Beall (1948) says that *D. plexippus* "freshly emerged in the autumn in Ontario start with a considerable fat reserve, some 30 per cent of the lean weight." Young migrants add even more; they have fat as high as 125% of lean weight. Migrants taken in New Orleans, presumably from a long journey, have fat only 2% of lean.

NYMPHALIS CALIFORNICA

Yothers (1913) reported that in 1912, *N. californica* larvae at a number of places in Washington, Idaho, and British Columbia were "by the millions," defoliating *Ceanothus velutinus*. At Clayton, Washington, the larvae had eaten all the leaves, and the branches were entirely bare except for the millions of larvae. On July 7, 1912, he found millions of larvae on Moscow Mt., Idaho. Then on July 13th, all the larvae and pupae were gone from the place of infestation. "The caterpillars had evi-

dently not migrated, for all around as far as I could see the *Ceanothus* had not been touched. Even had the caterpillars migrated that would not explain the absence of the chrysalids. I think that the total disappearance of these caterpillars and chrysalids was no doubt due to birds."

On May 11, 1973, in Del Puerto Canyon, 22-23 rd. mi. W of Patterson, Stanislaus Co., Calif., I noted *N. californica* larvae all over most of the *Ceanothus integerrimus* bushes, stripping some bare, although some bushes were untouched (all stages of instars above ca. second or third). (Adult hibernants were fairly common there on March 11, 1973.)

William Neeley (pers. comm.) saw "millions" of *N. californica* one day during the first week of August, 1962, on the summit and sides of Triple Divide Peak, Yosemite, California, flying east from the SW San Joaquin drainage in a band $\frac{3}{4}$ -1 mile, $1\frac{1}{2}$ -30' in height, from noon to three pm; some were landing.

EXTRA SPECIES JOINING MIGRATION

One puzzling aspect of butterfly migrations, especially those in the tropics, has been the accompaniment of many species in the migration. For example, Welling (1959) notes one migration consisting "of just about everything imaginable," flying from N to S in the Yucatan Peninsula, especially *Anteos clorinde* and *A. maerula*, with *Eunica tatila* and *E. monima*, made up the bulk of the migration. Also *Papilio* sp., *Heliconius charitonius*, *Eurema* species, many *Libytheana carinenta*, *Danaus* sp., a few blues, *Phoebus*. He mentions (1964) *Eunica monima*, *Agraulis vanillae*, "and a few other odds and ends" accompanying a large migration of *Kricogonia castalia lyside* in Yucatan. Such observations appear to be explained by the following observation recorded by Poulton (1929, 1930): Mr. F. Muir observed "the sweeping up of the non-migrating butterflies on a Papuan island when a migratory flight from another island passed over it. In this instance, in which more than a single species was involved, it is evident that the social stimulus, and this alone, availed to compel the non-migrating butterflies to become migrants—with such success indeed that the island was comparatively depleted of these species after the migratory stream had passed."

MAJOR SPECIES OF MIGRANTS

The following species from Williams (1930) appear to be frequent, conspicuous migrants: *Catopsilia florella* (Africa), *C. sennae* (Americas), *C. statira* (South America), *C. pyranthe* (India, Ceylon), *C. pomona* (Ceylon, India, Java), *C. crocale* (Ceylon, India), *Belenois severina* (Africa), *B. mesentina* (Africa, India), *B. java teutonia* (Australia), *Appias albina* (Ceylon, India), *A. paulina* (Ceylon), *Ascia monuste* (Americas), *Danaus plexippus* (circumcontinental), *Vanessa cardui* (world-wide), *Nymphalis californica* (U.S. and Canada), *Libythea bachmannii* (U.S.), *L. carinenta* (Americas), *L. labdaca* (Africa), and the moths *Urania leilus* (Neotropics) and *U. fulgens* (Central America). It is perhaps of significance that these species belong to the Pieridae, Libytheidae, and Nymphalidae, a set of families that are evolutionarily inter-related (Shields, unpublished libytheid study.) Also, all, of course, are common to very common species, and many are known to be strong, fast fliers with two or more broods and comparatively rapid generation time. One migrant female *Vanessa cardui* produced 685 larvae in captivity (Schrader, 1928).

It is known that *Ascia monuste* has a dark form (*phileta*) that is the migratory phase (Klots, 1951). I have noticed that *Vanessa cardui* migrants are larger with brighter colors than the non-migrant phase, generally. A parallel might be drawn here with Uvarov's phase theory of locusts, with solitary and migratory phases of the same species differing in morphology, coloration, physiology, and behavior (Poulton, 1929; Williams, 1957).

START OF A MIGRATION

Despite innumerable reports of butterfly migrations in progress, rarely have observations of their actual commencement been recorded. The circumstances surrounding the start of the flight are expected to shed the most light on the illusive cause of butterfly migration and perhaps the origin of the navigation of the flight as well. Accordingly, the details of published accounts of the start of migration that I have been able to locate are given in full.

Sir Guy Marshall recorded that the migration of *Catopsilia florella* was actually taking place from a Rhodesian valley (Poulton, 1931).

Pitman (1928) gives an account of the crowded breeding-grounds of *Belenois mesentina* in the West Nile Province of Uganda, from which start the great southward migrations in Uganda and Kenya. In a grassy plain some 2 miles broad and 7-10 miles in length their foodplant (*Maerua oblongifolia*, Caparidaceae) was abundant "in full, tender leaf and flower," in March 1928 following a few heavy thunder-showers after which the weather continued exceptionally hot and dry. The area had evidently been burned out some weeks previously. Most of the foodplants were leafless; "larvae and chrysalises were to be seen everywhere, as also countless thousands *in cop*," soon after emergence. "I have never before seen such countless myriads of butterflies, and as far as the eye could see there was a shimmer of white just above the surface of the ground." Preceding this emergence the West Nile was in drought for nearly twelve months. The adults were of small size, evidently due to starvation from the over-population. No actual migration of the adults, however, was observed.

Heape (1931, pp. 148-150) records a migration of *Catopsilia* (?) in the states of Ceará and Piauí, Brazil, the end of January or early February, 1915, after the rains had started, from the mangrove swamps on the right bank of the River Camocim; "the flight was somewhere to the north of west." 36 hours after the flight began, it was followed on horseback by two men for 4½ days and 125 miles. "They diminished markedly in numbers the further westward they travelled." By the time the town of Sao Pedro was reached, some 50 miles further, the flight had ceased ("petered out"). One observer returned to Camocim and learned "there that the flight continued to emerge from the mangrove swamp for forty-eight hours after he had left the place, and then a heavy storm put an end to those which still remained in the swamps and the flight stopped."

"It is of particular interest to note that the route followed by these gentlemen passed over the high ground east of the Paranaíba River, and from there on to Sao Pedro, through sandy hills and rocky flats where the scrub was dried up, although it was the rainy season; and all over this country large numbers of the butterflies were seen lying dead. They most certainly had not laid eggs there, and it was judged they fell from exhaustion while *en route*, leaving a trail of dead bodies."

Collenette (1928) witnessed the start of a migration of *Libythea carinenta*. Between Corumbá and Urucum, Matto Grosso, Brazil, November 1927, "extraordinary numbers" covered

muddy areas in the road all day long from November 16-21. November 22-23 was rainy and cool, with the mud practically deserted. Then on November 24, a bright and clear day, the migration started, many flying S and SSE starting about 7:30 am, while large assemblages were still on the mud. "At one such mud gathering, two or three in a minute rose and joined the passing stream, taking the general direction at once, without hesitation. In the instances which I was able to watch closely, there seemed to be no preliminary fluttering or walking about before taking to wing, and those which rose did not chase or play with those already in flight." None of the passing migrants were seen to settle on the mud, though they "frequently paused and fluttered over the gathering." He noted only three or four instances of pairing. At 9:45 am he left for Corumbá in the direction from which the *carinenta* were coming "in much the same numbers." "The insects quickly became fewer, and in about a mile I reached the drier vegetation, in which practically none were present, and where no migration was visible." He believed the swarm had "bred locally or had been attracted from the drier country in the neighbourhood."

Skertchly (1879) discovered the pupae of *Vanessa cardui* very numerous on grass blades between the mountains and desert in March 1869 west of Sowakin in the Sudan of Africa, soon after daybreak. "Presently the pupae began to burst, and the red fluid that escaped sprinkled the ground like a rain of blood. Myriads of butterflies limp and helpless crawled about. Presently the sun shone forth, and the insects began to dry their wings; and about half-an-hour after the birth of the first, the whole swarm rose as a dense cloud and flew away eastwards towards the sea. I do not know how long the swarm was, but it was certainly more than a mile, and its breadth exceeded a quarter of a mile."

Abbott (1951) records that John Garth found *Vanessa cardui* perhaps near the start of a migration at Santa Maria Bay, Baja California, 600 miles SSE of San Diego. "Thousands" of adults were seen, many of them emerging. Many flew south a short distance to the edge of the cliff, then north again to the breeding area, but no migration as such was in progress. It is probably significant that they were observed in a migration year, and at about the same dates as in California.

Emmel and Wobus (1966) noted *Vanessa cardui* near Florissant, Colorado in large densities (but no mass movement) from mid-July to mid-August, 1965. Then on August 22nd they "began

flying about due south and south-southwest in vast numbers, and this mass movement, involving every individual seen, continued until August 25. By this date, almost all *V. cardui* had left this area but scattered individuals were observed flying south through August 28, when a cold front moved in and stopped all butterfly activity for several days." The flight started at 7:00 am to nearly dusk. Between September 1-19, *V. cardui* continued moving southward in reduced numbers. On September 20th a severe cold front moved in, apparently curtailing the migration.

END OF A FLIGHT

Williams (1930, p. 353) says migrants "frequently pass over large areas of land apparently entirely suitable for their inhabitation, but continue on and on as long as the migration hysteria lasts, and may end up in the open sea or in entirely inhospitable lands where breeding is impossible." "There are records of swarms of butterflies reaching the coast and flying steadily on out to sea" (p. 389). At Arolla, Switzerland, August 6, 1903, *V. cardui* in large numbers of big faded specimens "invaded the district and settled down, each on its own piece of land, to alternate duties of fighting with a neighbour and egg-laying" (Williams, 1930).

LACK OF RETURN FLIGHTS

It seems a paradox that migrations of *V. cardui* and others are unidirectional and nearly constant when they occur, yet return flights to replenish the migrant gene pool appear rare or non-existent. If accurate, somehow the species is repetitive in behavior in migration years (a mass exodus serving as a "safety valve" on the population). Thus perhaps most but not *all* of the migrant population departs during years of migration.

EFFECTS OF OVERCROWDING

According to Poulton (1902), "The [migration] instinct . . . compels the individuals to move together in vast masses in the same direction, rather than to scatter and fly in all directions." "The suggestion is made that the crowded masses, resulting from over-production and inability of enemies to cope with the increase, are injurious to the species, because it is likely that food-plants would be checked for years or even killed out altogether in certain localities, while the heaps of dead individuals would encourage the attack and rapid spread of bac-

terial foes." The advantages derived from removal of the surplus from an overcrowded area would account for the development by natural selection of the instinct to move. Otherwise, there would be a destruction of the species in the area of overproduction.

Poulton (1921) quotes Trimen as saying, "The instinct to emigrate probably exists in a dormant state in all species liable to outrun the food-supply in any part of their range." If the overcrowding is unchecked, it would threaten the existence of the foodplant over a wide area. Near Mombasa, Africa, *Libythea laius* and other butterflies "appear only in occasional years . . . after a period of prolonged and severe drought," [when parasites, diseases, predators at a low, vegetation lush, and numbers would thus build quickly.] In some cases the migrant has stripped the leaves and shoots of its foodplant, such as *Catopsilia florella* on *Cassia arachoides* in Griqualand West in 1881.

Heape (1931) says, "All the evidence I have gleaned from investigation of the voluntary movements of the higher animals points, to my mind, definitely to the conclusion that emigration [of butterflies] is induced by overcrowding and the scarcity of food" (p. 158.) "Whatever may be the cause of these mass movements the result is that thereby huge surplus populations are effectually disposed of and the world saved from the incalculable devastation they would cause if they lived" (p. 171). "I have already suggested that the access of virility which attends the growth of the gonads and the development of reproductive cells in the higher animals, may well be the exciting cause of that stimulus which urges towards adventure of such kind [migration]; and that the resulting condition of a horde of individuals so affected may attain to what we call hysteria. I further suggest that, in spite of the radical differences both in the sense organs and in the central nervous system of insects, a condition comparable to hysteria may similarly be induced in them" (p. 170). "These conditions [i.e., the periodicity of migrations] are probably of climatic origin and affect the quality of the food supply and so govern reproductive activity."

In observations of migrating Lepidoptera often the "genital products" are in a backward condition (i.e., immature), and a migratory flight is necessary for their full development. Thus the stimulus to migrate may be a physiological one (Poulton, 1929).

Chapman (1939) mentions that Gause talks of "relaxation oscillations" arising from a relaxation or a decrease of environmental resistance, followed by a sudden population increase causing outbreaks. In insects having a high biotic potential, this relaxation during a single generation may result in a population increase of outbreak proportions.

Alexander (1961, fig. 63) suggests that field crickets under high density, crowded conditions showed no male territoriality and dispersed widely, compared with individuals in isolation which developed male territoriality and dispersed little.

It should be mentioned that *Colias eurhytheme* often forms dense swarms numbering as much as some migrations of other species, but is not known to migrate unidirectionally (F. T. Thorne, pers. comm.).

INHIBITION OF STIMULI

Kennedy (1961) thinks "Migrants are distinguished by a transient accentuation of locomotor functions with depression of vegetative functions, such that the insect now travels." "The Nielsens listed the reflex patterns of adult *Ascia monuste* 'living in a territory' as feeding, mating, egg-laying, basking and cleaning, and reported failure to respond to the appropriate stimuli for any of these when the butterflies were engaged in unidirectional flight elsewhere." "Ecologically, migration sometimes looks like an alternative to diapause when conditions will no longer permit growth, development or reproduction." "The internal inhibition of certain reflexes is the behavioural component of a whole physiological syndrome."

POST-TENERAL EXODUS FLIGHT

According to Johnson (1960), "Whenever the start of a 'mass migration' of insects has been described—and this is very rare in spite of a voluminous literature—the insects have always been making either their first flight as new adults or one very soon afterwards." He makes reference here to *Catopsilia crocale*, *C. pyranthe*, *Ascia monuste*, *Vanessa cardui*, and *Nymphalis californica* doing so, from the breeding site. There was only ca. 1 hour between emergence and migration in two instances of *Vanessa cardui*. "The initial orientation of the insect in flight is probably 'imprinted' during the teneral period, or determined at take-off." "Too long an enforced wait before take-off, leading to sexual maturation or fertilization, apparently inhibits migration altogether in *A. monuste*."

OVIPOSITION

In *Catopsilia pyranthe* in Ceylon, "every female seemed possessed with the one insane idea of getting rid of her eggs with the utmost expedition . . . and then madly continuing her flight" (Poulton, 1921). *Belenois mesentina* females in a migration at Peradeniya, Ceylon, were often seen "to stop and lay eggs on bushes of *Capparis pedunculosa*, rejoining the migratory flight as soon as a few eggs had been laid" (Poulton, 1929).

SEX RATIO

Williams (1930, p. 344) says males mostly predominate in pierid migrations checked (24 cases), while females predominated in two instances (of *Catopsilia*). In five instances of *V. cardui*, females predominated (Europe), while in two instances males predominated (p. 345). A migration of *Catopsilia pyranthe* and *C. pomona* in Ceylon in November 1905 had the main flight 87% males, but later stragglers were almost entirely females (p. 346). (Males generally emerge first before females in butterflies.)

PARALLEL BETWEEN MAMMAL AND BUTTERFLY MIGRATIONS

Deevey (1960) delves into cause of lemming migrations; they are neurotically sick during migration. The "shock disease" causes them to die in numbers "from their own excitement." Food, predators, disease, and weather periodically relax a hold on lemming numbers. It is the younger lemmings that migrate. Also, the end result is a wipe-out (population crash) of migrating individuals largely, in lemmings (and certain insect migrations). When there are large numbers of rats, these display a "pathological togetherness" (i.e., prefer to live together, low fertility, shortened lives). In mammals, Christian (1950) reported that there is a sudden die-off in late winter and early spring following a population peak, due to the exhaustion of the adreno-pituitary system ("shock disease"). "The terminating factor is the attainment of a population above the carrying capacity of the environment." The population is under highly stressed conditions and taxes the adreno-pituitary system to the maximum.

Direct experimental evidence that butterfly migrations undergo a similar "shock disease" is lacking. However, there is observational evidence that this syndrome does in fact take

place. Bernheim (1917) records a massive *Libythea bachmannii* migration near Eagle Pass, Texas, September 4, 1916. "There were literally millions of them and many of them had evidently completed their allotted span of life as they were dropping from the air in large numbers. One particular specimen flew past, almost brushing my face, and, as I thought, alighted upon the ground. As I stooped to examine it the wings suddenly folded down tightly in front of the body and I picked the insect up quite dead." Heape (1931, pp. 148-150) reported large numbers of a *Catopsilia* (?) sp. lying dead after its migration through the territory, in Brazil. On April 15-20, 1973, I noticed fresh *Vanessa cardui* bodies forming windrows along the highway during a migration in the Eastern Mojave. Some appeared to fall dead to the pavement from the flight merely from the wind of passing cars. Hayward (1953) says that on December 26, 1951, there was an *Ascia monuste* migration in Argentina present in the millions, with thousands of dead on the ground, many in fresh condition.

POSSIBLE CORRELATION WITH SUN-SPOTS

Grant (1937) has noted a correspondence in years of outbreak (40 out of 60) in *Celerio lineata* moth migrations in Europe and North America. "In seeking for an explanation of the outbreaks of *l. livornica* and *l. lineata*, one must look for some large cause, wide enough in its effects to have influenced both continents simultaneously." She found some relationship between the outbreaks and 11-year sunspot cycles over a 100 year period (fig. 5). "The number of outbreaks would seem to rise from the minimum towards the maximum, and then fall away towards the next minimum . . .," with some exceptions. She also found a strong tendency for outbreaks to occur when a wet year has followed a dry year. Williams (1965, p. 158) found a tendency for simultaneous abundance or rarity in North America and Europe in *V. cardui* from 1865-1938, statistically more significant than Grant's *Celerio lineata* correlations! Williams, however, said he could find no apparent correlation in *C. lineata* and *V. cardui* outbreaks to sun-spot cycles. With *V. cardui* there were above average numbers at both the maximum and minimum sun-spots, with below-average numbers on rising and on falling periods in the cycle.

Brown (1974) mentions there are recent suggestions of interrelationships between solar activity, the Earth's magnetic field, and the weather. Periods of maximum sun-spot activity

show an 11-year cycle. Wood & Lovett (1974) found a highly positive correlation of drought years in Ethiopia and sunspot minima (from 1540 to 1974). Over a 72 year period there, "The rainfall clearly follows a cyclic pattern in which rainfall peaks and troughs precede the sunspot peaks and troughs by a few years" (i.e., to 2 years). "Thus, there is a strong statistical correlation between Addis Ababa rainfall and sunspot number, the rainfall peaks leading the sunspot peaks by an average of 1.3 yr." Thus there would indeed appear to be some correlation between *V. cardui* outbreaks and the sunspot cycle, i.e., occurring after several years following rainfall peaks and extreme droughts.

RAINFALL

Williams (1965, p. 23) says, "Painted Ladies breed during the winter along the edges of the great North African desert belt, and then move north in the spring across the rest of North Africa, the Mediterranean and Europe." In Ceylon, the NE monsoon starts in about October with very heavy rainfall. "This is followed immediately by great flights of butterflies," lasting for about 3 months, "and then, after a lull, there is a recrudescence of activity in March and April corresponding to the end of the north-east and the beginning of the south-west monsoons" (p. 53). At Portachuelo Pass, 3500', Venezuela, Beebe noted 250 species of butterflies "migrating" through; "the flights seem to be associated with the rainy season, which lasts roughly from April to November" (p. 44).

WIND

Of 367 recorded observations of directional flight by butterflies in which the direction of flight and wind had been recorded, there were little or no significant differences in proportion among flights with the wind, diagonally with and against the wind, across the wind, and against the wind (Williams, 1949).

DIRECTION OF FLIGHT

Williams (1949) notes that in the tropics, flights of the same species tend to recur in the same direction at the same season in different years. "On reaching an obstacle most migratory butterflies pass *over* it rather than *round* it. . . ." "Migratory butterflies have also at times been observed to follow the windings of deep valleys, of roads through forest, and of shorelines. . . ." "There are . . . a few observations of simultaneous flights of two or more species, each flying in a different direc-

tion through the same locality for many days, and each keeping to their own direction." The movements of both such species had no apparent effect on the other. It is often noticed that butterfly migrations cease or are much reduced when the sun is clouded. "Orientation is quite definite at midday in the tropics when the sun is so near the zenith as to be practically useless for horizontal orientations" (Williams, 1957).

Flights of migrants that follow the shore line and do not fly out to sea, e.g., *Ascia monuste*, *Erynnis zarucco funeralis*, and *Urania fulgens*, suggest that topographic features play a part in determining the success of a migration, rather than it being a totally suicide flight.

Welling (1964) found *Calpodus ethlius* in Panama in its migrations "does not adhere to one single direction, mention being made of it 'passing in almost every direction' in the course of a single afternoon and evening." He saw one migration going N to S, slowly changing from W to E, then finally changing from SW to NE in one hour. They were therefore flying circles within that particular grassy swamp.

A *Catopsilia sennae* migration continued to fly during a tropical thunderstorm with heavy rain but oriented randomly (Johnson, 1969, p. 155). In a migration of *Catopsilia statira* in Trinidad, Williams noticed that when he attempted to catch examples, "any butterfly narrowly missed was put off its direction by the excitement and flew off wildly in any direction. Other butterflies close at hand meeting this butterfly flying out of the general order would in turn become confused and sometimes follow it in its new direction. So that after several misses in succession I was surrounded by a number of butterflies flying in all directions. If I stopped attempting to catch specimens these would gradually pass away, and the regular direction of flight would be resumed" (Poulton, 1921).

I reported (1967, p. 112) that migrations of *Vanessa cardui*, *Danaus plexippus*, and a *Delias* sp. are known to pass over summits of hills and mountains. No "staying" at the hilltop was shown by these. One migration of *V. cardui* on Dictionary Hill summit flew upslope from the south, flew across the summit, and instead of flying down the other side flew up and out off the north slope. Others were seen to pass over the hill's shoulders. No concentration toward the summit by the flight was noted. This could be a "breakdown in territoriality" (F. T. Thorne, pers. comm.), as resident *cardui* continued to "hilltop" that day. Wright (1906, p. 37) records a migration of *V. cardui*

on top of "Grayback," 11,600', that was going due east. They flew up the slope of the mountain and upon reaching the top, where the crest dropped off suddenly, "they kept straight on as far as the eye could follow them, right up into the sky. . . ." A *V. cardui* migration was seen flying over a 1300m summit in Austria in 1877 (Williams, 1930).

Tulloch (1912) reports an *Atella phalantha* migration on Mauritius, on the Trou-aux-Cerfs, an extinct volcano. Immense numbers flying up the crater towards the east; at the top they flew to the other side of the crater, then downhill to the bottom, where they went "right-handed round the base of the volcano" until they reached where he had been before, where they went uphill. "In fact, the butterflies were all going on an endless round, up the hill, across the top, down again, and round to where they started." The atmosphere was very clear, bright, and hot; a westerly breeze was blowing.

Abbott (1951) says *V. cardui* in southern California fly to the NW mostly, but also NNW or N. He says one would suppose butterflies following a definite compass direction would fly across a canyon from rim to rim, but instead *V. cardui* flies down one side and up the other, "keeping about the same distance from the ground all the time." "Butterflies which approached the lee side of a hill, flying NW, changed their course when they came to the top of the hill, turning and flying against the SSW wind. While they were turning, one single butterfly was seen to keep on toward the northwest." He notes that some upon encountering a wall in their path rose in the air in a "spiral" until clearing the roof, proceeding then NW.

NAVIGATION

Vleugel (1952) believes that the sun is the governing factor in the orientation of butterflies, based on bird migration studies. He supposes that somehow the "migrating butterflies allow for the change of angle necessitated by the apparent movement of the sun." However, Williams (1965, p. 126) defeats the argument for a sun-compass direction that allows for the angle change necessitated by the apparent movement of the sun: (1) the migrant would have to allow for the rising of the sun each morning at a 180° angle from sunset as flights resume each morning in the same direction as the previous evening, (2) when delayed for several consecutive days by bad weather they still resume their flight in the correct direction, and (3)

they can migrate at mid-day in the tropics when the sun is overhead and therefore useless for direction finding. No known organ in insects seems likely to be sensitive to the Earth's magnetic field, according to Williams.

Perhaps a means of circumventing these difficulties is to assume that the freshly emerged migrant adults navigate by using polarized light at the time of day they would normally start exhibiting territoriality and "freezing" upon this angle (D. A. Watts, pers. comm.). This fixed polarization would overcome the problem of having to adjust to a changing sun angle throughout the day. *Vanessa cardui* spring migrations in northern Africa-Europe and in California both trend mainly NW (compare Williams, 1925, fig. 2 with Abbott, 1951, fig. 1), while in the southern hemisphere in SE Australia, *V. cardui kershawi* migrations fly predominantly S to SW during spring (August to November for some 7-8 weeks) (Smithers, 1969). *Vanessa* normally exhibits "hilltopping" and territorial behavior in the afternoon starting from 12:30-3:15 pm PST (Shields, 1967) but peaking in late afternoon, while feeding at flowers in the morning. The sun in the afternoon would be in the SW quadrant of the sky in the northern hemisphere (above the Tropic of Cancer) and in the NW quadrant in the southern hemisphere (below the Tropic of Capricorn) in the spring, so that the *V. cardui* migration direction would be "fleeing" at nearly right angles from the sun's incident light. This is along the direction of the plane of polarized light, as can be seen with a Polaroid sheet. I.e., in the morning in the northern hemisphere above the Tropic of Cancer, the plane of polarization rotates from N to E and S to W, while in the afternoon it rotates from W to N and E to S. For *Libythea bachmannii* the majority of the migration records are toward the E or SE in July-September (SE predominant) in Texas., and *Libythea labdacæ* flies in March-May to the SW, SSW, S, SE, ESE in Nigeria and Gold Coast, with one record of *L. laius* in May in Tanganyika flying N (Williams, 1930). Here the *Libythea* would be using the plane of polarization to fly toward the sun. A summary of ca. 25 migrant species from Kodaikanal, S. India by Evershed (Williams, 1930, p. 297) showed primarily N-NE, S, SE movements in six species in February-March [sun slightly southward], northward and NE-E-SE movements in May-June [sun slightly north], and 100% southward movements of nearly all the species in August-November (primarily October) [sun southward to far

southward]. Waterman (1955) says that light from the sun as transverse electromagnetic waves is partly polarized by the scattering of light by air molecules. To the human eye, this polarization is nearly invisible.

Mazokhin-Porshnyakov (1969) says that sunlight is polarized up to 70-80%. It is known that various aquatic crustaceans, the horseshoe crab, some terrestrial arachnids, and winged insects (certain Coleoptera, Hemiptera, Diptera, Hymenoptera, Trichoptera, and Lepidoptera) react to light polarization; both faceted eyes and simple ocelli are sensitive to polarized light. Honeybees can quickly learn to distinguish between two light beams polarized in different planes. Impulses within the optic lobes arose following a rapid 90° rotation of the polarized plane in honeybees. "According to Autrum and Frisch, the insect's ability to recognize different polarization planes is due to the radial distribution of the visual cells in the forms of a rosette. If we suppose that each visual cell is sensitive to polarized light in a given plane, then the whole rosette would act as a polarization analyzer." "Electron microscopy investigations of the rhabdom in insects and other arthropods . . . revealed that polarization analysis is a property related to the rhabdomeres' periodic ultrastructure which repeats itself in different ommatidia. . . . Organic molecules absorb light when it is polarized in the same direction as the longitudinal axis of the chromophore. Since the visual pigment molecules are regularly oriented within the rhabdomeres . . . and absorb more strongly when the light is polarized in preferred planes (dichroism), they could . . . act as a polarization analyzer" (p. 141).

Vowles (1950) noted that ants (*Cataglyphis*, *Monomorium*, *Myrmica*) maintained a constant angle of orientation relative to the plane of polarization of light, in experiments (field and lab). With *Myrmica*, by altering the plane of polarized light with a Polaroid sheet, a new angle was assumed by the ant to the dorsal beam of plane-polarized light (his graph), but not to one of ordinary light. A tortricid larva (*Archips cerasivorana*) that crawled toward the sun was induced to turn 90° by placing a polarizing sheet over it as it moved, with continued maintenance of the new course under the influence of the polarizing sheet (Wellington, 1955). "It is common to see both larvae and adults fall victims of heat stroke on a sheet of paper while they are engaged in ineffectual circling movements in response to rapid changes in the sky," due to clouds or smoke. ". . . the sun is primarily a heat source, and . . . the plane of polarization is

the primary means of maintaining orientation to the sun . . . when an insect crosses an open space in daylight," according to his experiments. "The compound eye of an insect is fixed on the head and seems to be especially suitable for recognizing the polarization over the whole sky at once, providing that we assume that it can act as an analyzer of polarized light" (Frisch, 1950, pp. 90-96).

NIGHT MIGRATION?

Reports of butterflies migrating at night may be spurious unless actually observed to do so. The only migration claimed to be observed taking place at night that I am aware of is "Eagle Clark's observation . . . that . . . *V. cardui* flew toward England from the Continent against a wind *at night*" (Shannon, 1915, p. 618). Kendall & Glick (1972) record many instances of diurnal butterflies collected at visible and ultraviolet light at night, including some migrant species. "Evidence indicates most diurnals must be disturbed from their resting places before they appear at induced light" (p. 275). Thus, claims of butterflies migrating at night because they were taken at lights are probably unjustified. Their high density in the vicinity would account for some turning up at light. An exception would seem to be a report by Kingdon (1932) of a ship 87 mi. at sea with *Vanessa cardui* at lights at midnight thought to have come on board the previous hour. There was a strong off-shore wind, and had been all day. However, Williams (1930, p. 342) noted individuals of a swarm of *Pieris brassicae* resting on the surface of the ocean and taking flight when disturbed, so it is possible the *cardui* were roosting nearby on the water. Even large-scale migrations take place only from sunrise or somewhat later (start) until sunset or dusk (cease) (Williams, 1930; Hayward, 1953; Smith, 1972). Birds can use celestial navigation in their migrations (Wallraff, 1960) but butterflies do not appear to do so.

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ATRYTONOPSIS HIANNA BIOLOGY AND LIFE HISTORY IN THE OZARKS

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ABSTRACT

The ovum, first and final instar larva, and pupa of *Atrytonopsis hianna* (Scudder) are described and illustrated. The biology of the Ozarks populations is given and the association between *A. hianna* and *Hesperia metea* Scudder is discussed.

INTRODUCTION

IN THE MISSOURI AND ARKANSAS OZARKS *Atrytonopsis hianna* (Scudder) occurs in local colonies in woodland clearings, cedar glades, or forest edges in close association with beard grass (*Andropogon gerardi* Vitm.). This is the only known food plant for *A. hianna* in this region. This is also the food plant of *Hesperia metea* Scudder and these two species are consistently found together in the same localities. We have reared *A. hianna* on numerous occasions from both Missouri and Arkansas populations. The illustrations are from specimens collected near Warsaw, Missouri.

MATERIALS AND METHODS

Ova were obtained by confining wild females in nylon chiffon bags over potted plants of *Andropogon gerardi*. Larvae were reared on potted plants of this grass and on others that had been planted outdoors and enclosed in screen wire coverings. A Wild M5 stereomicroscope with drawing tube and photo-tube attachments was used in preparing the illustrations of the ovum and first instar larva.

DESCRIPTION OF EARLY STAGES

OVUM: Width 1.25 mm, height .80 mm. Color bright lemon yellow when first laid changing to pale brown with pinkish accent dorsally. Micropyle coral red. Eclosion in seven to eight days.

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FIRST INSTAR LARVA: Head and prothoracic shield deep reddish purple, shiny. Freshly emerged larvae yellow, after feeding all but abdominal segments nine and ten turn pale green. Surinal plate with long white setae, body thinly covered with long white hairs, prothoracic color paler. The first instar larvae are active silk spinners, trailing a silken thread as they move about. Stadium period: nine days.

SECOND INSTAR LARVA: Head dull orange brown, mandibles darker brown. Head thickly covered with minute white setae. Prothorax white, prothoracic shield, slender, shiny black. Body color dark green, posterior segments dull brown, anal segment with thick black setae, rest of body sparsely covered with minute black setae. Integument translucent. The second instar larval tent is constructed by fastening the top two thirds of two grass blades together. The top of the tent is left open. Stadium period: nine days.

THIRD INSTAR LARVA: Head pale orange brown, midcranial inflection edged with paler lines, stemmata black, mandibles dark brown. Head thickly covered with a mixture of short and longer brown setae. Body color pale pinkish brown with green undertones due to translucent integument, abdominal segments eight and nine paler, segment ten dull brown. Prothorax creamy white, prothoracic shield, slender, shiny black. Stadium period: nine days.

FOURTH INSTAR LARVA: Head dull orange brown, stemmata and mandibles black. Head thickly covered with short pale setae and a few longer white hairs. Body color bright pink dorsally, anal segment darker, almost black, with some long black hairs. Rest of body covered with minute white setae, integument translucent. Abdominal areas dull green. Prothorax creamy white, prothoracic shield black, slender. Stadium period: nine days.

FIFTH INSTAR LARVA: Head light brown, frons pale orange, labrum dark brown, mandibles and stemmata black. Head thickly covered with short white setae and a few longer white hairs. Body color lavender pink dorsally, bright pink ninth abdominal segment, anal segment grayish brown with long black hairs, rest of body thinly covered with short white setae. Prothorax white, prothoracic shield, slender, shiny black. Abdomen grayish white. Spiracles tiny pale yellow dots. The fifth instar larvae live in a three- to four-inch tube composed of several grass blades fastened together, open at the top and bottom. These tents are

usually constructed within six inches of the tips of the leaves. Feeding slows up greatly in this instar with the larvae spending many days aestivating. Before transforming to the next instar the larvae seal the tent at top and bottom. Stadium period: variable up to 19 days.

SIXTH INSTAR LARVA: Head deep red, mandibles black, frons and area below midcranial inflections deep reddish orange. Head granulose and thickly covered with short white setae. Body color light pink dorsally, brighter on abdominal segments eight and nine, tenth segment darker brown dorsally. There is an inconspicuous middorsal gray line. Abdomen and prothorax pale translucent gray. Spiracles pale orange, inconspicuous. Prothoracic shield, slender, shiny black. The body now has a downy appearance due to a thick covering of soft white hair. The larvae in this instar pass through alternate periods of eating and aestivating. The larval tent is the same as in the fifth instar. Stadium period: variable, an average of six to seven weeks.

SEVENTH (FINAL) INSTAR LARVA: Head width 3.5 mm, deep reddish purple, granulose, unmarked but with brown shading below laterofacial suture lines, deeply cleft at midcranial inflection, mandibles black. Head covered with short reddish setae and longer white hairs. Position and size of stemmata as illustrated. Length of mature larvae 29-32 mm. Body color pale pinkish lavender dorsally, abdominal segments eight and nine pale pink, anal segment depressed, pale glossy brown. Prothorax pale gray, prothoracic shield dark brown, surface granulated. Abdomen pale grayish white, thoracic legs pale brown. Entire body covered with long yellowish white hair, shorter on the abdominal areas. The prolegs have orange hair and the anal segment has bright orange setae, coarser and shorter than on rest of body. Only the last abdominal spiracles are noticeable, they are pale brown. Final instar larvae have two small wax pad areas beneath the posterior segments of the abdomen. The final instar larvae feed consistantly once the cooler damp weather of September begins and by early October the larvae seal themselves in a nest among the leaves at the base of the food plant to pass the winter as mature larvae, pupating early the following spring.

PUPA: Length 18.5-20 mm, width at widest point of wing cases 4.5-4.75 mm, width at eyes 3.50-3.65 mm. Wing cases light brown with olive tint. Head, eye cases and upper thorax darker brown. Thoracic spiracles ruby red. Tongue case deep brown, detached below wing cases. Abdominal segments light orange

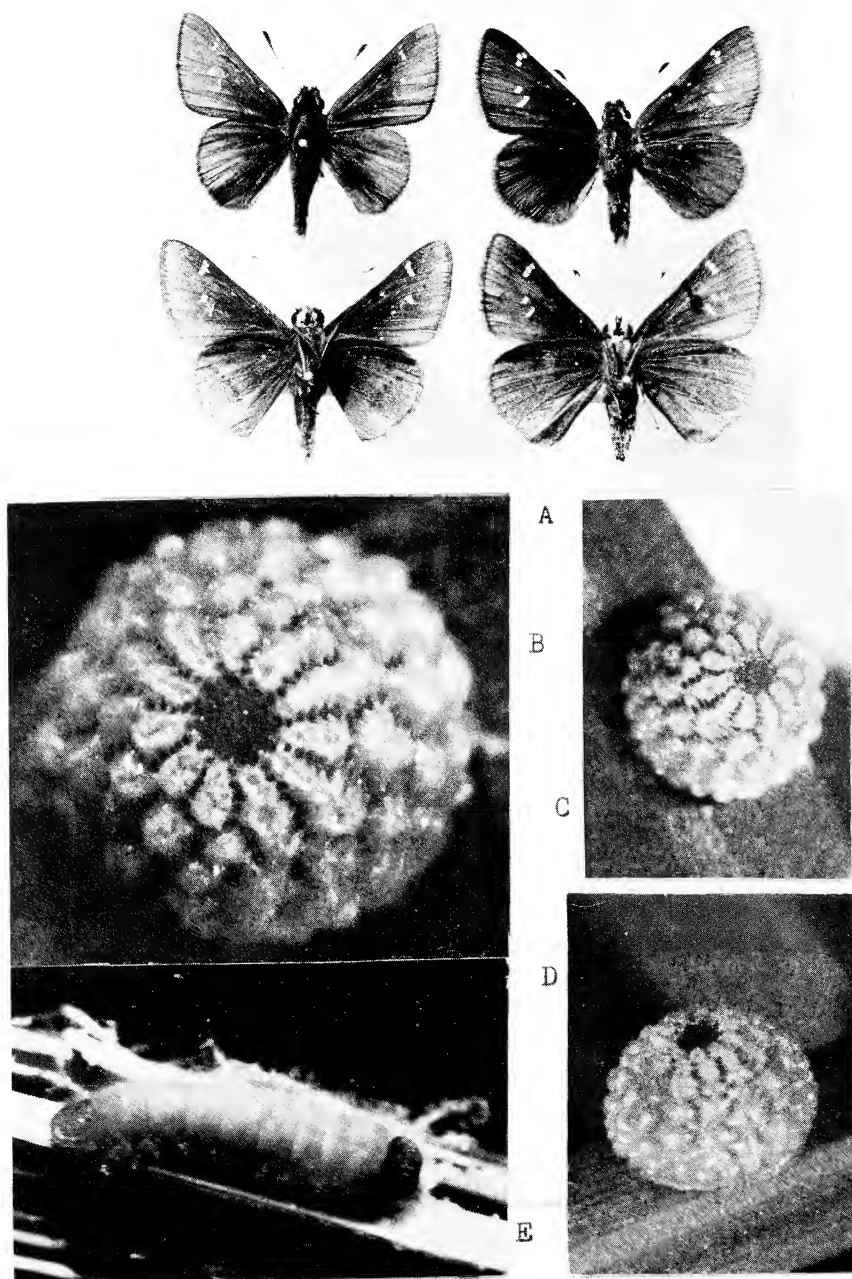


Fig. 1.—*Atrytonopsis hianna* (Scudder), A, male and female, ventral and dorsal view of specimens from Warsaw, Missouri. B, C, D, different aspects of the ovum. E, mature larva.

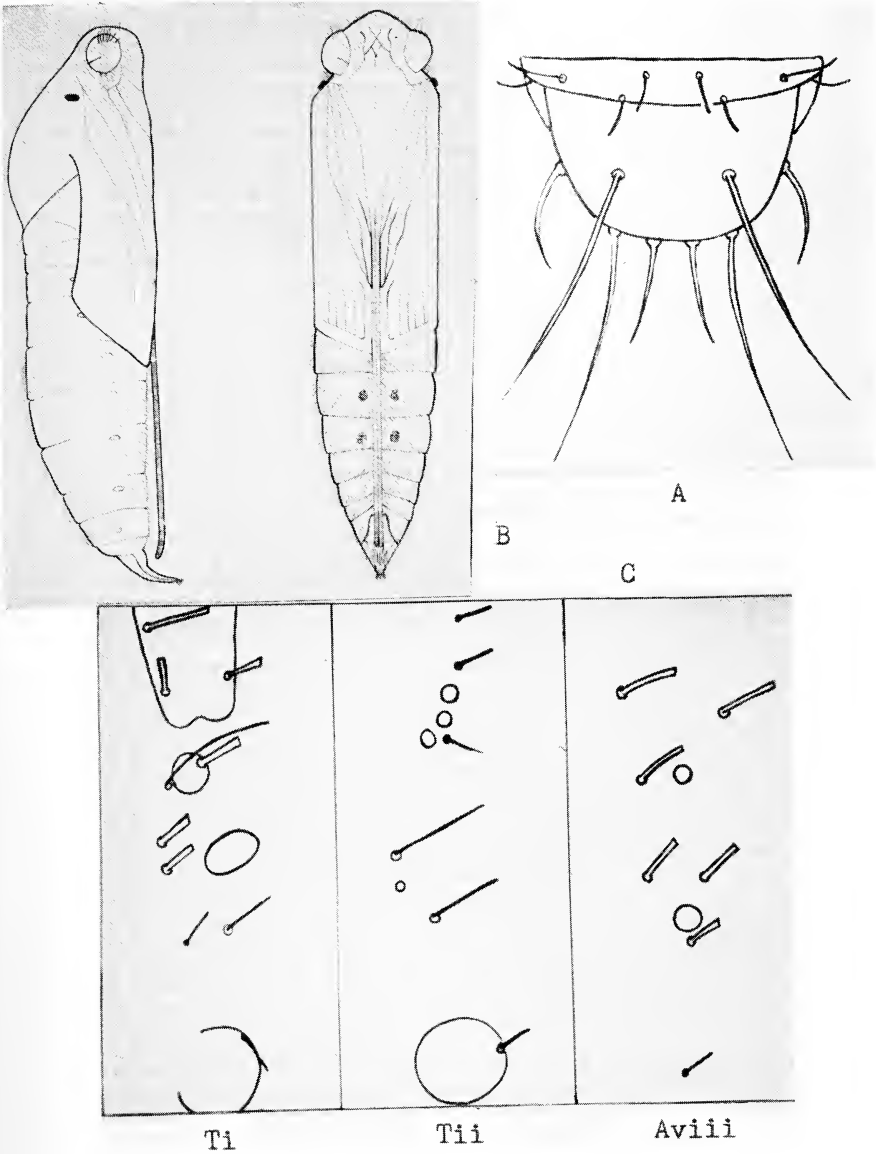


Fig. 2.—*Atrytonopsis hianna* (Scudder), A, first instar suranal plate. B, pupa, ventral and right lateral aspect. C, first instar setal maps of prothorax, mesothorax, eighth abdominal segment, all in left lateral aspect.

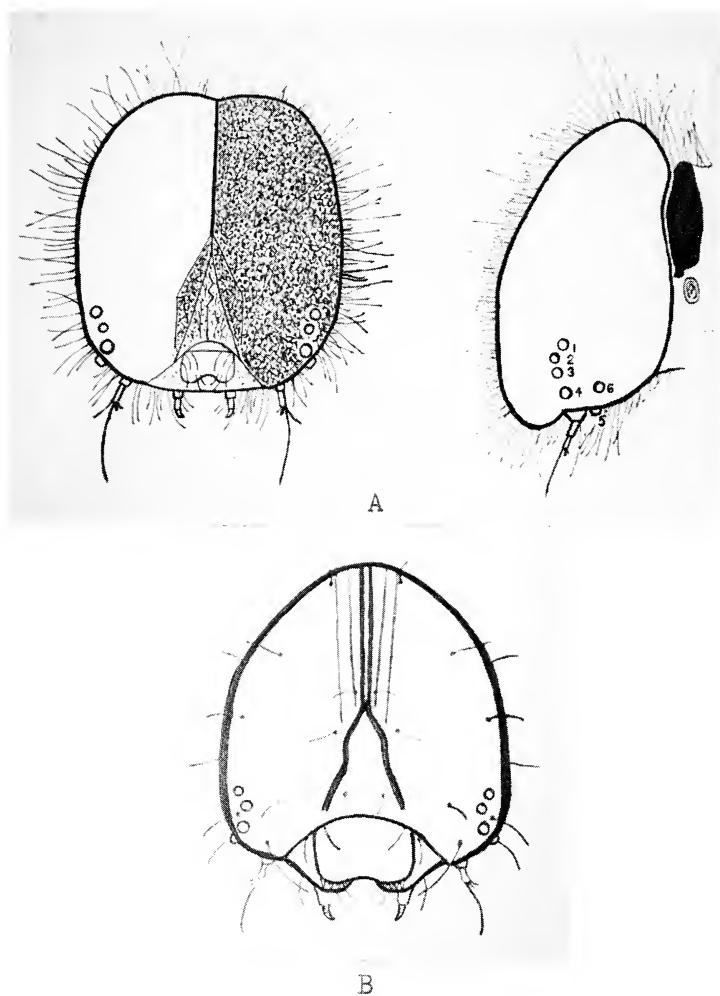


Fig. 3.—*Atrytonopsis hianna* (Scudder), A, head of final instar larva, frontal and left lateral aspect. B, head of first instar larva, frontal aspect.

with pink overcast, intersegmental folds pale orange brown. Cremaster and anal segments darker brown. Cremaster 2.75 mm in length, strongly curved ventrally, without hooks but densely covered at the tip with stiff brown setae. Pupation occurs in the base of the *Andropogon* clumps, one to three inches above ground level in a sealed case of silk and grass leaves.

DISCUSSION

In the introduction it was mentioned that *A. hianna* occurs consistently with *H. metea*. Both species are univoltine flying for only a few weeks in the spring but *metea* normally begins emergence one or two weeks ahead of *hianna*. The first *hianna* normally appear during the first week in May at Warsaw, Missouri (earlier in Arkansas) and the imagines have disappeared by the end of May. While both species utilize the same food plant their different feeding and resting positions seem to effectively preclude any severe competition for the host plant. While *metea* in its later instars lives in a tent in the base of the grass clumps *hianna* is living in a tent from one to several feet above ground and does not appear to enter the base of the plants until ready to hibernate after feeding is completed in the autumn. *A. hianna* is an avid flower visitor and females are best collected by searching the flowers of *Verbena*, *Camassia*, and *Fragaria* growing in the vicinity of *Andropogon*. Males exhibit strong "perching" tendencies and will dart out at any passing butterfly or insect that remotely resembles a female *hianna*. Both sexes are wary and not easily collected. The numbers of imagines present from year to year varies greatly but to date no parasites have been bred from any of the wild larvae collected.

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LARVAL MIGRATION OF *HYLES LINEATA* (FAB.) (SPHINGIDAE)

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LARVAE OF *Hyles lineata* (Fabricius) were observed in mass migration on April 4, 1974, 17 miles south of Furnace Creek Ranch, Death Valley National Monument, Inyo County, California at an elevation of 300 feet. These larvae were traveling in a westward direction with a maximum concentration of approximately fifteen individuals per square meter. The width of the migration was approximately one fourth mile and the length is unknown. During the march, larvae fed on the prostrate lobed leaves of *Chorizanthe rigida* (Torr) T&G (Polygonaceae), a little low growing annual, and then moved on to another plant when these were gone.

Twenty larvae were taken and reared to adults on apple (*Malus* sp.). All were in the last instar, although they had much feeding to do before burying themselves to pupate.

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NEW FOOD PLANT FOR
DARAPSA PHOLUS (CRAMER)
(SPHINGIDAE)

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TIETZ (1972) listed the following plants for *Darapsa pholus*: *Kalmia angustifolia*, *Nyssa sylvatica*, *Rhododendron nudiflora*, *Rhododendron viscosa*, *Tradescantia virginiana*, *Viburnum dentatum*, *Viburnum lentago*, *Viburnum opulus*.

These records were taken from Beutenmüller (1895), Morris (1862), Harris (1839), J. E. Smith (1779) and others (Eliot and Soule, 1902; Fernald, 1886; Baynes-Reed, 1881). I myself checked additionally the following: Forbes (1948), Holland (1903), Rothschild and Jordan (1903), Clemens (1859), Fernald (1886, re-checked), Draudt in Seitz (1931) and Hodges (1971). The food plants for *D. pholus* mentioned in these publications are the following: Forbes: *Azalea*, *Viburnum* and "reported from other food plants, probably in error for *D. myron* and *cnotus*"; Holland: *Viburnum*, *Azalea*; Rothschild and Jordan: same as those of *Ampeloeca myron* (*Ampelopsis*, *Vitis*) which is certainly in error; Clemens: *Azalea nudiflora*; Fernald: *Ampelopsis quinquefolia*, *Viburnum lentago*, *Viburnum dentatum*, *Viburnum opulus*, *Nyssa multiflora*, *Azalea viscosa*, *Azalea nudiflora* (it seems that the error concerning *Ampelopsis* originated with Fernald); Draudt in Seitz: *Ampelopsis Vitis* (probably on the authority of Rothschild and Jordan); Hodges: *Azalea Viburnum* species.

Tietz (1972) also gave *Viburnum* as a food plant for *D. myron* besides *Ampelopsis* and *Vitis*. Hodges (1971) too mentioned *Viburnum* for *D. myron* and it may be that the erroneous record of *Ampelopsis* and *Vitis* for *D. pholus* was created in a kind of exchange between food plants of *myron* and *pholus*. I did not check in which of the many papers quoted by Tietz for *D. myron* this *Viburnum* record originated.

One plant group, however, has never been mentioned among

the food plants of *D. pholus*: *Vaccinium* spp., our common blueberries. During field work in 1974 at Queen's University Biological Station at Chaffeys Locks, Leeds Co., Ontario, we found all stages of *D. pholus* associated with *Vaccinium* spp. and it is not unreasonable to suppose that *Vaccinium* may be a general food plant for the species, the more so as several *Viburnum* species are also common around Chaffeys Locks but *D. pholus* was not found associated with them.

Data for the immatures collected in 1971 are: egg on blueberry at Washburn, Ontario, 25 July, hatched and reared successfully on blueberry; third instar larva on blueberry on Snake I. in L. Opinicon, Chaffeys Locks, Ontario, 26 July, reared successfully on blueberry; a freshly-emerged, unmated female moth flushed from a blueberry patch at the Station around noon, 8 July, eggs infertile.

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NOTES ON ARCTIC AND SUB-ARCTIC COLLECTING

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The ensuing remarks are not intended as an all-inclusive coverage of arctic collecting. They relate to certain areas of which the author has some knowledge and offer comments, hopefully useful, to those collectors who might be anticipating a trip to the northlands. Travel to the Far North becomes easier every year, and more and more collectors will be traveling north in search of the "treasures" to be found there.

There are several items which every collector going to the Far North should keep in mind. Of primary importance is seasonal variation. In any given year, the flight period for a species may be quite different from the year before or the year following. Some species appear to be biennial.

Weather conditions are extremely variable from year-to-year, and from day-to-day. Overnight temperature drops of 60°F are not uncommon.

During June and July, the prime collecting months, extended or continuous daylight occurs depending upon latitude. Thus it is useless to take along a light trap for moths during this period, although a trap may be of use in some areas in August.

For personal comfort, protection against biting insects is essential. Some of the best collecting is in muskegs (bogs). Entrance into such areas by any warm-blooded body is an open invitation to a host of mosquitoes and flies. My suggestion for dress is as follows: Mid-calf rubber boots (for both bogs and tundra areas), heavy weight but loose Levis, light shirt under a light weight Nylon windshirt, cap or hat with visor, and an army-style O.D. headnet. The boots will assure dry feet. The loose heavy jeans should frustrate the bugs in any attempt to bite legs. Tuck the jeans inside the boots. For some reason, mosquitoes don't seem to be able to penetrate effectively Nylon cloth, hence the windshirt. Army-style headnets, available from

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surplus outfits, cover head and shoulders and tie under the armpits. This avoids the use of insect repellent. Generally speaking, I have found repellents nearly useless in arctic regions and in comparable areas in the Rocky Mountains. Although smelly, the oldtime Oil of Citronella appears to be more effective than anything else, with Cutters a close second. The latter, however, attacks some plastics and one must use it with caution. Light gloves may be necessary when collecting in deep bogs. Oil of Citronella rubbed on the hands, especially the backs of the hands, will generally suffice for protection against the angry stilettos.

Clothing should be chosen in anticipation of wet weather and a wide temperature variation. The mean temperature at Churchill, Manitoba in the summer is about 50°F. In McKinley Park, Alaska, I have experienced a temperature drop from nearly 90°F to 30°F over an eight-hour period at the end of June.

Finally, avail yourself of a "native guide" if one exists. Local collectors can indicate very quickly the good and bad spots. Many of the arctic species tend to be quite local in habitat, and frequent areas that one familiar with more southern latitudes would bypass. Collectors with experience in the Rocky Mountains (high-altitude species) are perhaps the best prepared to "smell out" the habitats of the arctic species.

Generally speaking, the arctic mountain passes are at low elevations (between 3000-4000') with altitude-treeline about 3000' or less. Above certain latitudes, no trees occur, only scrub. This is true at 58°45'N (sealevel) at Churchill.

Arctic and subarctic collecting can be at the same time, both very rewarding and very frustrating. The reward is in the variety of species that can be found; the frustration is in trying to collect them because of weather conditions. In this paper, some of the prime collecting areas are described along with the problems associated with visiting these spots.

From my experience, albeit somewhat limited, the best seasons for collecting appear to occur in odd-numbered years following a cool and wet year. In central Alaska, many of the desirable species of *Boloria* and *Oeneis* seem to fly only during odd-numbered years, although occasional examples may be taken in even-numbered years. Another feature to recognize is that the daylight hours are different from more southern latitudes. Twenty-four hour daylight or near daylight is the rule in June and July. For this reason, the collecting season begins in mid-June and is virtually over by the end of July in most locali-

ties; a far different situation from the Rocky Mountains, for example, when prime collecting is from mid-July into August.

Weather conditions are of major importance, and at best are unstable and unpredictable. Anyone planning an arctic trip should allow enough time to be in any given collecting area during the better part of the season. It is not unusual for bad weather to continue for a week or more. Thus one should have a month's time, at least, available for arctic trips. Coastal Alaska, especially the southern coast, the Hudson Bay area (Churchill), and northeastern Canada (Mt. Albert, Gaspé, etc.) are subject to stationary low pressure areas during the summer, which may persist for days or weeks. In the Churchill area, when the ice breaks up on Hudson Bay at the end of June or in early July, cold weather (in the 30's), fog, and drizzle are the rule. These conditions may persist for three days to a week with no collecting possible. By contrast, interior Alaska, north of Fairbanks and south of the Brooks Range can be hot and clear (temperatures in the 90's) at the same time of year. South of Fairbanks (McKinley Park, etc.), coastal conditions prevail.

Alaska:

Alaska is accessible by car, boat, and air. For one who has the time, it is well worth the extra days of travel to drive the Alaska Highway. Weather permitting, there is good collecting starting north of Edmonton, Alberta (Hwy. 43). The Alaska Highway proper begins at Dawson Creek, B.C. The first 88 miles are paved. The section through British Columbia and the Yukon Territory to the Alaska border is very well maintained gravel. The last leg of the highway from the border to Fairbanks is paved. Since the major portion of the road is gravel, one should take some necessary precautions. These include extra spare tires, beyond the usual spare, plastic headlight protectors, a 1/4" hardware cloth or other screen across the front of the car to deflect stones, chassis undercoating, and a pad over the fuel tank, for rear-mounted tanks, to prevent stone punctures. A tool kit and spare parts should be carried, as although there are gas pumps every 50-100 miles, repair service is hard to find and expensive. Because of the fine dust, a heavy-duty air cleaner is strongly recommended. Other than dust and possible flying stones, when passing or being passed, the only other hazards are occasional washouts after heavy rains. These are usually repaired within 24 hours and generally present little problem for passenger cars, but may cause difficulty for recreational vehicles and cars with trailers. The main washout danger area

appears to be the 300-mile stretch between Dawson Creek and Ft. Nelson, British Columbia. Extra gasoline should be carried, as many of the service stations open late in the morning and close early in the evening, especially on weekends. A VW or similar car is ideal for the trip, although a bit cramped.

Except for Whitehorse, Yukon Territory, accommodations along the highway are minimal. There are a number of turnout areas and several campgrounds, however, and tent or recreational vehicle camping is no problem. One should plan on four nights camping between Dawson Creek and Fairbanks if any amount of collecting is to be done along the way. Members of the American Automobile Assn. should obtain the booklet available on the Alaska Highway, as it contains an excellently detailed map.

The best collecting spots that I found are muskegs, willow bogs, and the emergency air strips. The latter are well-marked clearings just off the road. They are covered by low vegetation and usually present a good supply of wildflowers. One must get out into the centers of the bogs and investigate the little islands of black spruce, for these will yield *Erebia disa* and *Oeneis jutta*. Various species of *Boloria* frequent the willow bogs.

Figure 1 shows the main road and major collecting areas in Alaska, in terms of accessibility. Nome, Anatumuk Pass in the Brooks Range, and the North Slope are accessible by air via Wien Airlines. One should check at Fairbanks for flight schedules. One of the major areas is Eagle Summit, which is 109 miles north of Fairbanks on the Steese Highway. As of the summer 1971, the first 44 miles of the road were paved with the remainder gravel. The road continues past Eagle Summit to the Yukon River. Some of the species of interest at Eagle Summit and 12 Mile Summit just to the south are: *Oeneis melissa*, *polixenes*, *bore*, *Erebia youngi*, *magdalena*, *discoidalis*, *disa*, *fasciata*, *Boloria polaris*, *titania*, *chariclea*, *youngi*, *freijs*, *frigga*, *napaea*, *distincta* (for the lucky), *Papilio machaon*, *Colias nastes* and *Parnassius eversmanni*. The summit areas are above-treeline tundra. Both north and south of them are below-treeline muskeg areas which should be investigated for *Plebejus optilete*, *Colias palaeno*, *Hesperia manitoba*, *Boloria*, *Erebia*, and *Oeneis*.

Generally speaking, the major habitats, and this is true of the arctic regions in general, are black spruce muskegs and willow bogs in the Taiga Zone, and the open Tundra Zone. The boreal forests are usually too dense to permit collecting and appear

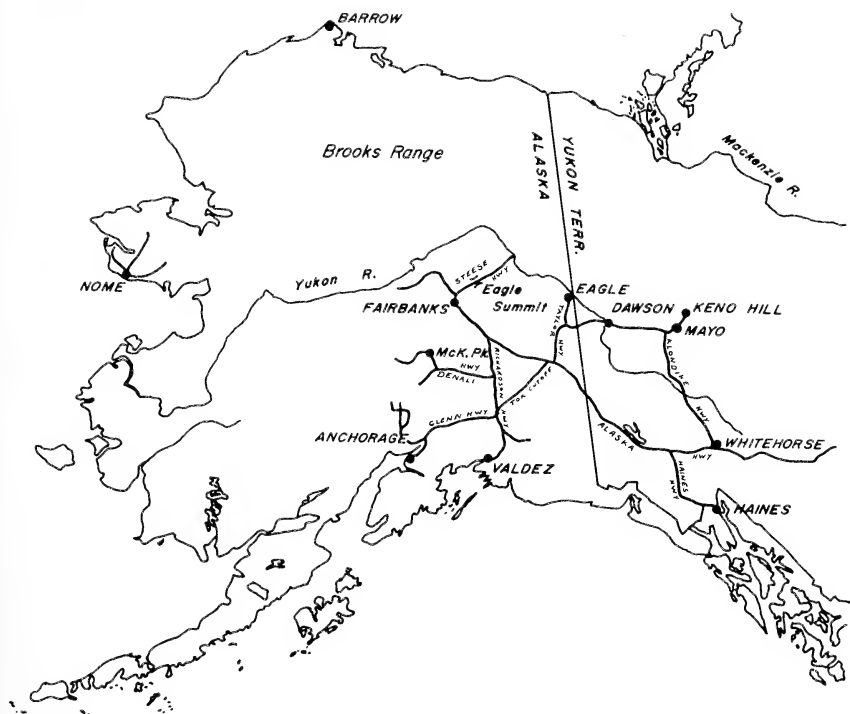


Fig. 1.—Map of Alaska and Yukon Territory. Highways are shown as the thicker solid lines.

to harbor very few species.

South of Fairbanks, the Richardson highway affords good collecting in spots. At Paxson Jct. (mile 185.5), the Denali Highway leads west to McKinley Park, 161 miles away. Although it was being "improved" in 1971, the Denali was an accumulation of chuckholes loosely connected by gravel. I would not recommend travel on it except in a light, but tightly-sprung vehicle. It is by far the worst major road that I have ever driven. Along the highway, one finds *Erebia rossii*, *Boloria eunomia denali*, and a variety of other species. The Denali Highway in McKinley Park is well-maintained and collecting is excellent, especially in the vicinity of the several Pass areas. Collecting, however, is *by permit only* from the National Park Service. Generally these permits are available only to university or museum personnel engaged in specific studies. Thus unless one wishes to tour the Park, which is quite beautiful and uncluttered, it is not a recommended trip because of the highway and the restricted collecting.

Toward Valdez and Anchorage, some interesting species can be obtained, but collecting is difficult because of adverse weather conditions. Snow at higher elevations (above 2500') is not unusual in June and July.

I have not found collecting at Haines very productive, although the dark coastal race of *Pieris napi* occurs there as well as *Anthocaris sara alaskensis*. I have collected both species there in early July. The Haines Highway will be covered in the Yukon Territory discussion.

Other areas of interest include spots along the Taylor Highway from the junction with the Alaska Highway to Eagle, Alaska. Charter flights can be arranged into remote locations, although bad weather can sometimes maroon the luckless collector in remote spots for extended periods of time.

*Yukon Territory, Northern British Columbia,
Alberta, and Northwest Territories:*

The most easily accessible collecting in northern Alberta, British Columbia, and the southern Yukon Territory is via the Alaska Highway and Highways 43, 34, and 2 from Edmonton to Dawson Creek, via Whitecourt, Alberta. An alternative route to Alaska is from Prince George to Prince Rupert, British Columbia. There are a number of spots along Highway 16 that will yield interesting species. At Prince Rupert, one enters the "Alaska Marine Highway." This is the ferry system which oper-

ates between Prince Rupert, B.C. and Skagway, Alaska, with stops at Ketchikan, Wrangell, Petersburg, Juneau, and Haines. The trip is quite scenic and takes about 36 hours. It is fairly expensive. The cost from Prince Rupert to Haines for two people and a small car is in excess of \$200, excluding meals. Ferry transport is also available from Seattle and Vancouver to Anchorage and other ports, at additional expense.

At Haines, Alaska, one enters the Haines Highway, which is approximately 160 miles long. The initial portion in the Alaska panhandle is paved. The remainder through a small corner of B.C. and the Yukon Territory is well-maintained gravel. The road joins the Alaska Highway at Haines Junction, Y.T. Entering the main portion of Alaska by this route eliminates over 900 miles of gravel-road driving on the Alaska Highway. The best collecting appears to be in the area between Kathleen Lake, Y.T. (mile 142) and Haines Jct., Y.T. (mile 159). Such species as *Oeneis bore*, *Euphydryas anicia helvia*, *Erebia epipsodea remingtoni*, *C. tullia* ssp., *Colias philodice vitabunda*, and *Parnassius phoebus* ssp. can be taken. Chilkat Pass, B.C. at mile 65.3, although appearing to be good habitat, I found completely devoid of butterflies.

Additional areas in the Yukon Territory are served by the Klondike Highway, which leaves the Alaska Highway just west of Whitehorse, Y.T. and meanders northwest to Dawson, and then west to Chicken where it joins the Taylor Highway to Eagle, Alaska. A spur goes to Mayo Lake and Keno Hill. Other areas can be reached by Charter flight. Essentially all areas in the Northwest Territories must be reached by air. The Mackenzie Highway from Peace River, Alberta does serve a few areas in the southern portion of the N.W.T. including Dawson Landing and Fort Providence on Great Slave Lake, Fort Simpson on the Mackenzie River (by a spur route), and Yellowknife, also on Great Slave Lake (north shore).

Two primary collecting areas are the Richardson Mountains in the western section of the N.W.T. and Baker Lake in the eastern section. A highway has been proposed that will skirt the Richardson Mts. allowing access to that area by car. Baker Lake, reached by air, is a choice spot in that *Colias boothi* is taken there, as well as a number of other species.

The Pas-Churchill, Manitoba:

In addition to his own experiences, the author has drawn on the papers by the Chermocks (1968) and Masters (1971) in

preparing this section. Acknowledgment is made here to these sources without subsequent mention.

The region between The Pas and Churchill is of interest for a variety of reasons. It is easily accessible. There are a number of subarctic and arctic species. There are good living accommodations.

The Pas is served by highway 10 which continues north another 100 miles to Flin Flon. Where land has not been cleared for agricultural purposes, it is a black spruce and muskeg area, much like northern Maine, dotted with lakes. Some of the indigenous species are *Colias gigantea*, *Boloria eunomia*, *Papilio machaon*, *Erebia* species, *Oeneis jutta* and *macouni*, *Coenonympha tullia*, etc., as well as species associated with more southern latitudes. It is a community of some 6000 with stores, motels, and a small museum. It is also the point of embarkation by rail to Churchill on the west coast of Hudson Bay. No roads go to Churchill, so one has to take the train from The Pas, or the plane from Winnipeg. In 1973, the round-trip fare, per person, was about \$134.00 by air from Winnipeg and about \$37.00 by rail from The Pas (coach).

If one possesses an adventurous spirit, then by all means take the train. Those of a more sedate mien are well advised to fly. The rail distance from The Pas to Churchill is 510 miles and requires about 22 hours in transit, as the train makes extended stops to unload freight and change crews at Thicket Portage, Thompson, and Gillam. At these stops, the train is literally invaded by the local Indians, to whom a rail coach is tantamount to a movie matinee. This is not conducive to sleeping, as the Gillam stop occurs just after midnight. The train schedule is typically: leave The Pas 10:30 AM Mon., Wed., Fri.; leave Churchill 5:30 PM, Tues., Thurs., Sat. In either direction, the Gillam stop is at midnight.

It is also possible to drive from The Pas to Thompson and fly from there to Churchill, or board the train. This saves about 175 miles of train travel, but increases driving time. During the peak of the summer months, there are some flights, but not on a daily basis, from The Pas to Churchill.

Churchill is actually a dual community of Churchill and Ft. Churchill. The two are about 3 miles apart and the overall population is just over 3000. There are several "motels" and hotels as well as stores in Churchill proper. My wife and I stayed at the Whaler's Co-op "motel" which has comfortable housekeeping units and makes very reasonable weekly rental

rates. It is located between the railroad and the Churchill River about 100 yards from the tundra. Thus right on the edge of prime collecting territory, which is between the railroad and the river from town to about 4 miles south at milepost 505 on the railroad.

Tent camping on the tundra is possible, and the Chermocks did so. They wrote an amusing account of some of their experiences. Because of the weather, which can turn miserable for days on end, and the mosquitoes and flies, this is not recommended. After spending a hot day of collecting and fighting the biting insects, it is a welcome relief to come back to a hot shower and a comfortable bed. During sieges of bad weather, temperatures hovering just above freezing are common. Incidentally to preserve one's sanity, a headnet is *essential* at Churchill, particularly after the sandfly hatch. Figure 2 illustrates some of the "friendly" creatures that inhabit the area and lust for the blood of visiting lepidopterists.

A rough map of the area is shown in Figure 3. The Subclimax Tundra area affords the best collecting for *Erebia rossii inornata* Leussler, *Boloria polaris* (Bdv.), and the endemic *Oeneis*. *O. jutta* is in the little stands of black spruce and tamarack. The remaining species are in open areas. The Taiga Zone south of milepost 507 on the railroad offers the best collecting for most of the remaining endemic species, although there is some exchange of species between the Taiga and Tundra Zones. When they first appear on the wing, *Colias nastes* and *hecla* can be found a mile or more into the Taiga, along the railroad right-of-way (cf. Masters, 1971, p. 8).

Although the Climax Tundra to the east and south of town, and north to Cape Merry is profusely covered with wildflowers, I found it for the most part, devoid of butterflies, at least until mid-July when we departed Churchill. Scenically it is a striking area of granite boulders, flowers, mosses, and lichens. An excellent view of the ice on Hudson Bay as well as Churchill Bay is afforded from this area. It is well worth a visit just for the panorama it provides. One small area just at the edge of town yielded *Erebia theano canadensis* Warren, *Colias nastes moina* Strecker, and *Plebejus aquilo lacustris* Freeman.

To cover the various habitats completely, about 8-10 miles of walking per day is necessary. This may be reduced, however, by using the local bus or taxis. In the early morning, I frequently took the bus to Dene Village and began collecting along the Ft. Churchill railroad spur to where it joins the main line. From



Fig. 2.—Photograph of some of the “friendly” creatures which add to the “joy” of arctic collecting. These are from Churchill, Manitoba. The head-to-tail length of the central fly is 2 cm.

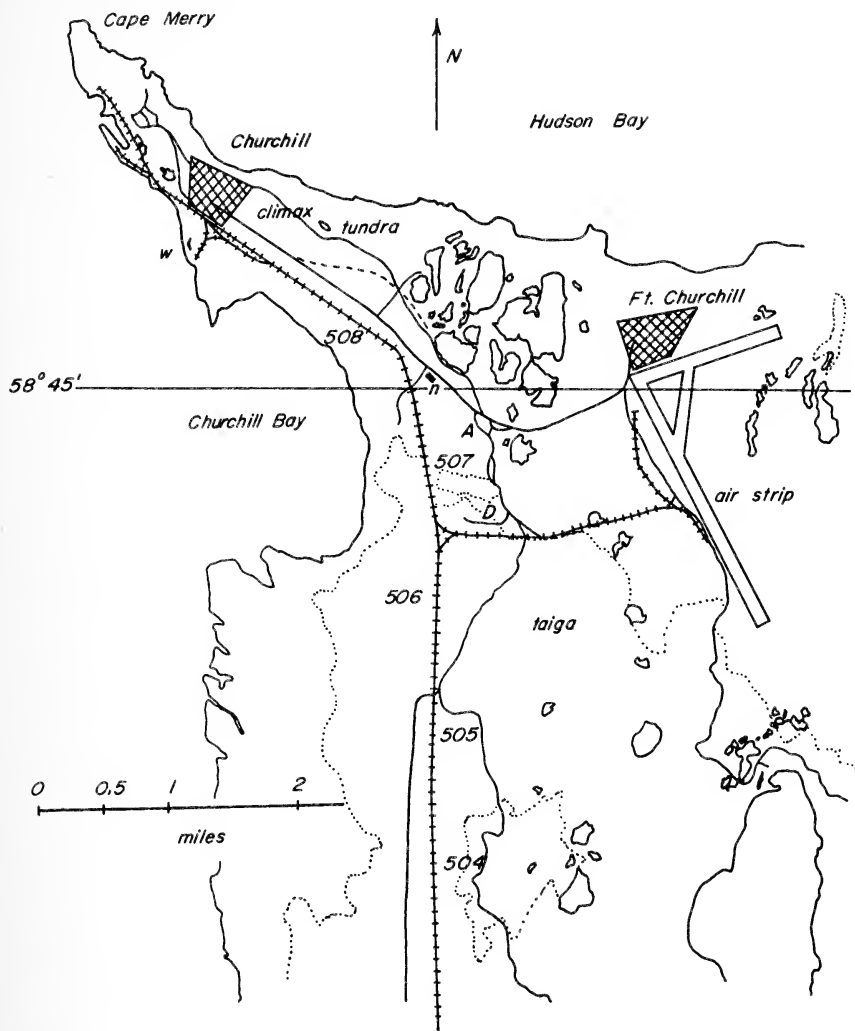


Fig. 3.—Map of Churchill, Manitoba area. W indicates the Beluga Sport Whaling Motel. A and D are respectively Akudlik and Dene villages. n indicates the old naval building. The numbers are mileposts along the railroad. The fine dotted lines represent the separation between the Tundra and Taiga Zones.

there, one can walk south along the tracks to mile 505 and then retrace steps and continue north across the tundra into town. The North Star Bus Lines, Ltd. provides regular service between Churchill and Ft. Churchill, with stops at Akudlik and Dene Villages.

Rental cars are available, but this is a waste of money. I believe in the philosophy ascribed to A. B. Klots, that is, if you are riding in a car, you can't be in the field collecting.

On warm mornings when the temperature is about 50°F, collecting begins at 9:00 AM; on cooler days, the bugs don't get out until about 10:00 AM. By 3:00 PM on cool days and 4:00 PM on warm days, collecting is over. This is quite different from interior Alaska, where I have collected from 7:00 AM until 9:00 PM. At Churchill, as long as there is full sun and the temperature is above freezing, butterflies will fly. I have collected in 35°F temperatures in mid-July. A warm day is when the temperature reaches 55-60°F.

Because of its interest to the collector and the accessibility of Churchill, a checklist is now provided including overall dates of flight. Seasonal variation is extreme so no attempt has been made to list peaking of flights. Masters (1971) made an honest attempt to do this, but when I collected in 1973, the species peaked much earlier than he indicated. Some years, however, are quite retarded. In 1973, the ice broke up in the vicinity of Churchill much earlier than normal and the Beluga whales returned three weeks ahead of schedule. In 1972-73 winter was exceptionally mild, after a cold and wet summer in 1972.

CHECKLIST — Churchill, Manitoba Butterflies

<i>Hesperia manitoba borealis</i> Lindsey	30-vi—3-vii	L
(Biennial on even years?)		
<i>Pyrgus centaureae freija</i> (Warren)	17-vi—14-vii	E
<i>Colias g. gigantea</i> Strecker	25-vi—9-viii	M
<i>Colias hecla hecla</i> Strecker (rare)	11-15-vii	L (Type Locality)
<i>Colias nastes moina</i> Strecker	26-vi—9-viii	L (Type Locality)
<i>Colias palaeno chippewa</i> Edwards	24-vi—9-viii	M
<i>Pieris napi</i> ssp.	16-vi—15-vii	E
<i>Glaucopsyche lygdamus</i> ssp.	Several reports, no dates	E
<i>Lycæides argyrognomon scudderii</i> (Edwards)	no dates	L
<i>Plebejus aquilo lacustris</i> Freeman	15-vii-73	L
<i>Plebejus optilete yukona</i> (Holland)	9-14-vii-73	L

<i>Boloria eunomia tricularis</i> (Hübner)	23-vi—9-viii	M	
<i>Boloria f. freija</i> (Thunberg)	10-vi—15-vii	E	
<i>Boloria frigga saga</i> (Staudinger)	17-vi—1-viii	E	
<i>Boloria polaris</i> (Boisduval)	20-vi—28-vii	E	(Biennial on odd years)
<i>Boloria titania boisduvalii</i> (Duponchel)	1-vii—9-viii	L	
<i>Erebia disa mancinus</i> Doubleday	9-vii-73	M	(1 pair — only record)
<i>Erebia d. discoidalis</i> (Kirby)	15-vi—10-vii	E	
<i>Erebia rossii ornata</i> Leussler	10-vi—16-vii	E	(Type Locality)
<i>Erebia theano canadensis</i> Warren	2-23-vii	L	(Type Locality)
<i>Oeneis borel taygete</i> ssp. (??)	15-vi—16-vii	E	(See Text)
<i>Oeneis jutta</i> ssp.	20-vi—15-vii	E	
<i>Oeneis melissa semplei</i> Holland	12-vi—2-viii	E	
<i>Oeneis p. polixenes</i> (Fabricius)	12-vi—2-viii	E	

Casuals and Strays

Papilio glaucus canadensis Roth. & Jordan (1) G. S. Brooks collector*. 1940.

Colias eurytheme Boisduval G. S. Brooks collector, 1942. Ferris saw what appeared to be a female of this species in the Taiga Zone, July, 1973.

Pieris protodice ssp. Bdv. & LeC. (1) G. S. Brooks collector*, 1942.

Pieris rapae (L.) (1) J. H. Masters collector, 3-vii-70.

Boloria selene ssp. (1) A. B. Klots, *in litt.*

Cynthia cardui (L.) 30-vi—15-vii-73 C. D. Ferris collector (common). (Migrant)

Nymphalis antiopa (L.) (Stray)

Nymphalis m. milberti (Godart) (Stray)

Lycaena species (probably *dorcas* ssp.) (1) 3-vii-52 in R. D. Bird field notes, see Masters (1971).

E = species which appear early in flight season; M = species which appear in middle of flight season; L = species which appear late in flight season. Actual appearance dates vary from season-to-season. (1) = single specimen record.

*These specimens have apparently been lost or destroyed.

Boloria chariclea ssp. has been recorded from Churchill, but probably has been confused with *titania*. At one time, the two taxa were considered conspecific by some authorities, and I believe that this has caused some of the nomenclatorial confusion in the Churchill records. Out of a lot of well over 100 specimens of *titania* which I took in 1973, four could be assigned to *chariclea* based upon facies. I choose to consider these as pale *titania*. A similar confusion zone between *titania* and *chariclea* exists in several parts of Alaska.

Masters (1971) asserts that two subspecies of *Oeneis jutta* occur at Churchill. *O. j. alaskensis* Holland, he claims flies on even numbered years, and *O. j. ridgingiana* Chermock & Chermock flies on odd numbered years. This situation needs more study, as there is an unpublished Chermock name relating to the Churchill population of *jutta*.

A strange situation exists with *Oeneis bore/taygete*. This has been reported by various collectors as occurring at Churchill. I took a small series of what I thought was this insect. The veins on the undersides of the hindwings are clearly outlined in gray as in *taygete*. The ground color of the wings dorsally is paler than normal *polixenes*. Genitalic examination has proved these specimens to be *polixenes*. I have received specimens from other collectors sent as *taygete*, which on genitalic examination are *polixenes*. It appears then that two phenotypes of *polixenes* fly at Churchill. I have yet to see *taygete* from Churchill, although it may occur there.

My collecting included two species not recorded at Churchill previously: *Erebia disa mancinus* and *Plebejus optilete yukona*. A pair of the *Erebia* was taken at about 1:15 PM (CDT) in full sun in a clearing (cf. Masters, 1972, p. 4) at mile 506.5 on the railroad right of way on 9-vii-73. *P. optilete yukona* was found throughout the Taiga Zone in moist areas. It and *Pyrgus centaureae freija* are probably quite common and widely distributed, but overlooked because they fly close to the ground and blend in color so well with the mossy ground cover. Both are erratic fliers.

I suspect that nearly all of the endemic species recorded from Churchill, except perhaps for *C. hecla*, are common in suitable habitat at appropriate times during the season. My pair of *E. disa* may have been introduced via the railroad from one of the colonies at Gillam or elsewhere. One resident species which now appears uncommon is *Erebia theano canadensis*. The Chermocks found it abundant in the early sixties, but J. A. Ebner's collector in Churchill failed to find it during three successive seasons in the mid-sixties. (*in litt.*). Masters found it in 1969-70. In 1973, I did not find it in any of the locales from which it had been reported in the past. I did find several colonies at other locations, but it is a very local species and is tied to a "micro-habitat." One of Chermock's collecting sites has been destroyed by an Eskimo village housing development. Other areas have been ditched for drainage purposes and this has altered habitat. *E. theano* is probably common in remote areas that collectors have not yet penetrated.

The Churchill area is undergoing considerable development. The Subclimax Tundra Zone especially is being reduced by housing and radio antenna installations. The area between the railroad and the Churchill River is still virgin except for the

extreme northern end where the Whaling Centre is located. Most of the town growth appears toward the east and south toward the high Climax Tundra Zone. Evident in 1973, was the construction of a new hospital and a government-financed housing development. In spite of the encroachments of "progress," Churchill remains a fascinating place to visit.

Mt. Albert, Gaspé Peninsula, Quebec:

Mt. Albert's attraction lies in several species which are recorded from the tundra tableland on its top. The tableland is oblong, quite extensive, and virtually without distinguishing features except for a boulder pile at the center. It is very easy to lose one's sense of orientation. *Oeneis taygete gaspeensis* dos Passos, *Oeneis polixenes* ssp., *Papilio brevicauda gaspeensis* McDunnough, *Hesperia manitoba borealis* Lindsey, and *Pyrgus centaureae freija* (Warren) are recorded as well as a record in the 1940's for *Oeneis chryxus* ssp. A number of other species are found at the base of the mountain along the Ste. Anne River.

Mt. Albert is reached by a cut-off road from Highway 6 just northwest of New Richmond, Quebec. A resort hotel is located along the road across the river from the mountain. In contrast to Mt. Katahdin in Maine, as yet there is no restriction to collecting.

Getting to the top of the mountain used to be somewhat of a problem, as legally, one was supposed to have a Canadian guide. This situation has changed recently and access to the mountain is relatively easy. Trail maps can be obtained by writing: Direction Generale des Parcs, Ministère du Tourisme, de la Chasse et de la Pêche, Edifice G, Cité parlementaire, Québec, Qué., Canada, G1A 1R3 and requesting the brochure "Sentiers de Randonnée Pédestre, Parc de la Gaspésie." The brochure is published in French. There is a campground close to the trailhead, or one may stay at the resort hotel. There are several routes to the top now. The "Plaque Malade" trail is an easy hike through the trees to the top, but is longer than the Mt. Albert Trail ("Sentier du Mont Albert").

The optimum collecting time is quite variable. L. Paul Grey (Enfield, Maine) has made a study and feels that the best time is probably between July 6 and July 17 (*in litt.*). *Oeneis taygete* appear to fly for a very short period each year. On the other hand, John Johnstone (Willowdale, Ont.), (*in litt.*) has stated that there are two flights of *taygete*; one in the latter part of June, and another in July. Clear weather is essential for col-

lecting on the top of Mt. Albert. Making the trip on an overcast day will prove fruitless, as the bugs just don't fly.

Another region of interest is Labrador-Newfoundland. The author has not collected in this area, and has been informed that, at present, access into the most desirable areas is restricted because of mining interests. Richard Holland (1969) has described some collecting in this locality and mentioned the concomittant problems.

ACKNOWLEDGMENTS

The author wishes to express his appreciation to various individuals who provided him with general information on arctic collecting, and specific information on collecting areas prior to trips to northern locales. Included are James A. Ebner (Okauchee, Wisc.) and Dr. Kenelm W. Philip (Fairbanks, Alaska). The author, his wife, and Paul Grey spent a delightful and amusing several days at Mt. Albert in 1968, and mulled over the quixotic behavior of *O. taygete*.

Jim Ebner and Ronald L. Huber (St. Paul, Minn.) were especially helpful in providing data from Frank Chermock's notes on collecting at Churchill, Manitoba. Warren Kiel (Grove-ton, N.H.) kindly provided current information on the access routes to the top of Mt. Albert.

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KLOET & HINCKS' CHECK LIST OF
BRITISH INSECTS (LEPIDOPTERA) EDN. 2.
A REPLY TO CRITICISMS.

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OUR ATTENTION HAS BEEN DRAWN by Dr. J. G. Franclemont of Cornell University to a paper by Juraj Paclt (1974, *Jl Research Lepid.* 12(4):211-212) proposing corrections to some of the family-group names used in the Lepidoptera part of Kloet & Hincks' *Check List of British Insects* (Edn. 2, 1972). Since we are jointly responsible for the preparation of this revised, second edition, a reply from us seems appropriate.

The correction of Evergestiinae to Evergestinae is acknowledged, but the other proposals put forward are contrary to the provisions of the current *International Code of Zoological Nomenclature* (Edn. 2, 1964) and its amendments, 1974, *Bull. zool. Nom.* 31: 77-89.

Family No. 50, Endromidae, derives from the suprageneric term Endromidi proposed by Boisduval, 1828, *Eur. Lepid. Index meth.* (1): 50, which is based on the validly included genus-group name *Endromis* Ochsenheimer, 1810. Article 29(d) of the *Code* states: "Incorrectly formed stem. — A family-group name proposed before 1961 based upon an incorrectly formed stem is not to be amended for that reason if it is in general current use. Incorrectly formed names published after 1960 are to be corrected wherever they are found". The correct spelling of the name applied to family No. 50 therefore is Endromidae, as published in the *Check List*.

For the same reason the spelling of the family-group names Syntominae proposed by Herrich-Schäffer [1846] 1845, *Syst. Bearbeitung Schmiett. Eur.* 2: 49, Cerostominae, proposed by Börner, 1925, in Brohmer, *Fauna Dtl.* (Edn. 3): 375, Enico-

stominae, proposed by Heslop, 1938, *New bilingual Cat. Br. Lepid.*: 82 and Cemiostominae, proposed by Spuler, 1898, *Sber. phys.-med. Soz. Erlangen* 30: 33 are correct as published in the *Check List* and are not to be amended.

Paclt's proposals to alter the synonymy of a number of the family-group names are equally ill-founded, as reference to Article 40 of the *Code* clearly demonstrates.

"Synonymy of the type-genus. — When, after 1960, a nominal type-genus is rejected as a junior synonym (objective or subjective), a family-group name based on it is not to be changed, but continues to be the valid name of the family-group taxon that contains both the senior and junior synonyms.

(a) Conservation of certain names. — If a family-group name, changed before 1961 because of such synonymy, has won general acceptance, it is to be maintained in the interests of stability".

In family No. 11 for example, Limacodidae is the oldest suprageneric term, based on a validly included genus-group name; it was proposed by Duponchel [1845] 1844, *Cat. méth. Lépid. Eur.*: 84. It will be seen from Article 40 of the *Code* that the validity of the family-group Limacodidae is in no way affected by the synonymy of its type-genus *Limacodes* Berthold, 1827 with *Apoda* Haworth, 1809.

Even if the family-group name were still to be based on the oldest included genus-group name, as Paclt appears to suggest, then his proposed synonymy of Limacodidae with Apodidae would still be in error. *Heterogenea* Knoch, 1783, not *Apoda* Haworth, 1809 is the oldest included genus-group name and this was used by Hampson in 1918 as the basis of the family-group name Heterogeneidae.

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THE NOMENCLATURE IN AN IMPORTANT BRITISH CHECK LIST (1972)

PART 3: CORRECT GENDER FOR GENERIC
NAMES DERIVED FROM CLASSICAL WITHOUT
CHANGE OF TERMINATION.

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THE REQUIREMENTS OF THE INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE concerning the agreement of species-group names in gender seem not to be strange to the authors of the new catalogue: 'The endings of the valid specific names, where adjectival, have been changed in accordance with Article 30 of the Code of Zoological Nomenclature' (J. D. Bradley, D. S. Fletcher and P. E. S. Whalley in their Introduction, p. vii).

Let us tell that the problem of correct application of endings in species-group epithets affects not only combinations in which the gender of the generic name is either somewhat doubtful or at least hard to determine. It will affect, as seen immediately below, even many of those combinations in which the generic name is derived from Greek (or Latin) without change of termination.

Nematopogon (masc.) with *N. swammerdamellus* (not 'swammerdamella'), *N. panzerellus* (not -ella), *N. pilellus* (not -ella), and *N. metaxellus* (not -ella) included.

Diplodoma (neuter) *herminatum* (not 'herminata').

Nemapogon (masc.) with *N. granellus* (not 'granella'), *N. cloacellus* (not -ella), *N. albipunctellus* (not -ella), *N. personellus* (not -ella), *N. ruricolellus* (not -ella), *N. arcellus* (not -ella), and *N. picarellus* (not -ella) included.

Archinemapogon (masc.) *laterellus* (not 'laterella').

Acrocercops, a latinized Greek noun of masculine gender, should, according to the Art. 30, be treated as such (provided that the author of that genus did not decide to use his name as a noun of feminine gender).

Phyllonorycter (masc.) with about 50 species listed the majority of which (42) are treated as if *Phyllonorycter* were of feminine (!) gender.

Yponomeuta (masc.: cf. *toreuta*, a graver) with *Y. evonymellus* (not '*evonymella*'), *Y. padellus* (not -ella), *Y. malinellus*, *Y. cagnagellus* (not '*cagnagella*'), *Y. rorrellus* (not -ella), *Y. irrorellus* (not -ella), *Y. plumbellus* (not -ella), and *Y. sedellum* (not '*vigintipunctata*') included.

Euhypnomyeta (masc.) *stannellus* (not '*stannella*').

Ocnerostoma (neuter) *piniariellum* (not '*piniariella*').

Prays (masc.) *fraxinellus* (not '*fraxinella*').

Augasma (neuter) *aeratellum* (not '*aeratella*'). This genus is a member of the family *Coleophoridae* to which *Eupistidae* and '*Augasmidae*' were referred to as synonyms. The latter must, however, be corrected to *Augasmatidae*.

Goniodoma (neuter) *limoniellum* (not '*limoniella*').

Enicostoma (neuter) *obellum* (not '*obella*').

Levipalpus (masc.) *hepatariellus* (not '*hepatariella*').

Gnorimoschema (neuter) *streliciellum* (not '*streliciella*').

Crociosema (neuter) *plebejanum* (not '*plebejana*').

Olethreutes (masc.) with 14 species listed all of which are treated as if *Olethreutes* were of feminine (!) gender.

Archips (masc.) with 12 species listed all of which are treated again as if *Archips* were of feminine (!) gender. Note the correct usage of *A. podanus* (not '*podana*') in recent literature.

Clepsis (fem.) *melaleucana* (not '*melaleucanus*'). The remaining species listed bear names agreeing in gender.

Ptycholoma (neuter) *lecheanum* (not '*lecheana*').

Aleimma (neuter) *loeflingianum* (not '*loeflingiana*').

Chilo (masc.) *phragmitellus* (not '*phragmitella*').

Parapoynx (masc.) with *P. stratiotatus* (not '*stratiotata*'), *P. obscuralis*, and *P. stagnatus* (not '*stagnata*') included.

Pyrausta (masc.) with *P. auratus* (not '*aurata*'), *P. nigratus* (not '*nigrata*'), and *P. cingulatus* (not '*cingulata*') included.

Herpetogramma (neuter) *centrostrigale* (not '*centrostrigalis*').

Myelois (myeloeis, masc.) *cribrellus* (not '*cribrella*') and *M. cirrigerellus* (not -ella).

Homoeosoma (neuter) with *H. nebulellum* (not '*nebulella*'), *H. sinuellum* (not -ella), and *H. nimbellum* (not -ella) included.

Apomyelois (apomyeloeis; masc.) *bistriatellus* (not '*bistriatella*').

Ochlodes (gender prescribed: masculine; Art. 30: 'Names ending in . . . -odes . . . are . . .') with *O. venatus* (not '*venata*') as the only species listed.

Colias (fem.) *crocea* (not '*croceus*'). For details on the gender see Paclt (1951).

Malacosoma (neuter) *castrense* (not '*castrensis*').

Phyllodesma (neuter) *ilicifolium* (not '*ilicifolia*').

Cilix (masc.) *glaucatus* (not '*glaucata*').

Camptogramma (neuter) with *C. bilineatum* (not '*bilineata*') and four subspecies (*bilineatum*, *atlanticum*, *hibernicum*, *isolatum*) included.

Perizoma (neuter) with *P. alchemillatum* (not '*alchemillata*'), *P. bifasciatum* (not -ata), *P. minoratum* (not -ata), *P. blandiatum* (not -ata), *P. albulatum* (not -ata), *P. flavofasciatum* (not -ata), *P. didymatum* (not -ata), *P. sagittatum* (not -ata); and including also some distinct subspecies. The remaining two species listed (*P. taeniatum*, *P. affinitatum*) bear names agreeing in gender.

Anticollix (masc.) *sparsatus* (not '*sparsata*').

Abraxas (masc.) with *A. grossulariatus* (not '*grossulariata*'), *A. sylvatus* (not -ata), and *A. pantarius* (not -ata) included.

Ennomos, a Greek noun of masculine or feminine gender, should, according to the Art. 30, be treated as masculine (provided that the author of that genus did not decide to use his name as a noun of feminine gender). Note the prevailing usage of *E. subsignarius* (not '*subsignaria*') in recent literature.

Apocheima (neuter) *hispidarium* (not '*hispidaria*') and *A. pilosarium* (not -ria).

Biston (masc.) *stratarius* (not '*strataria*') and *B. betularius* (not -ria).

Selidosema (neuter) *brunnearium* (not '*brunnearia*'), ssp. *scandinavarium* (not -ria) and ssp. *tyronense* (not '*tyronensis*').

Alcis (masc.) with *A. repandatus* (not '*repandata*'), three subspecies (*repandatus*, *murarius*, *sodorensium*¹), and *A. jubatus* (not '*jubata*') included.

Pterostoma (neuter) *palpinum* (not '*palpina*').

Eilema (neuter) with *E. sororculum* (not '*sororcula*'), *E. griseolum* (not '*griseola*'), *E. caniolum* (not -ola), *E. pygmaeolum* (not -ola), *E. complanum* (not '*complana*'), *E. sericeum* (not '*sericea*'), *E. deplanum* (not '*deplana*'), and *E. lurideolum* (not '*lurideola*') included.

Eugnorisma (neuter) *depunctum* (not 'depuncta').

Eurois (euroeis; masc.) *occultus* (not 'occulta').

Eublemma (neuter) with *E. ostrinum* (not 'ostrina'), *E. parvum* (not 'parva'), and *E. noctuale* (not 'noctualis') included.

Pseudoips (masc.) *prasinanus* (not 'fagana'). The authors disregard apparently the revision of the Linnean type (Lempke, 1947), according to which *Phalaena Tortrix prasinana* Linnaeus is the Scarce Silver Lines (*Pseudoips*). On the contrary, *Pyralis fagana* Fabricius corresponds to the Green Silver Lines (*Bena*).

Polypogon (masc.) *strigilatus* (not 'strigilata'). The remaining species listed bear names agreeing in gender.

ERRATA

On page 211 of Part 1 of the present paper (*J. Res. Lepid.* 12: 211-212), the sentence beginning with 'Although' (lines 17 to 22) is to be corrected to the following effect:

Although both subfamilies are called actually *Plutellinae* and *Depressariinae* respectively, and although the genus *Cerostoma* Latreille, 1802 has been replaced as junior synonym by *Ypsolopha* Latreille, 1796, the above family-group names should be referred to as *Cerostomatinae* and *Enicostomatinae*.

¹ *Gen. pl. ex vocis (Insulae) Sodor-enses quae ad Insulas Ebudes vel Ebudas (= the Hebrides) pertinent.*

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ARTIFICIAL DIET: THE KEY TO THE MASS REARING OF *MEGATHYMUS* LARVAE

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TECHNIQUES FOR REARING *Megathymus* larvae utilizing yucca caudices were discussed by Wielgus and Wielgus (1973). As a medium for rearing, yucca caudices proved to be difficult to preserve in a wholesome state for prolonged periods, were obtainable only with great labor and generally not available to others, and were cumbersome and space-consuming.

Petterson and Wielgus (1974) discussed a method of introduction and acceptance of an artificial medium by *Megathymus streckeri* (Skinner) larvae. The biology of *streckeri* larvae made rearing on yucca caudices extremely difficult (and hazardous to the larvae during the transfer process) so a more suitable substitute was devised in the form of artificial diet and man-made containers. Simultaneous with rearing *streckeri* larvae, the artificial diet substitute was used successfully with the larvae of other *Megathymus* species.

In 1974, 52 *streckeri* and 30 *Megathymus texanus texanus* B. & McD. ova were obtained and the newly-hatched larvae successfully started and established on artificial diet. Later that same year, several *Megathymus ursus ursus* Poling ova were collected and the newly-hatched larvae were also started and established on artificial diet with no difficulty.

Megathymus species split into two natural groups based mainly upon larval biologies, but also upon distinct pupal differences. The first group ("tent-builders") includes all of those species whose larvae construct and maintain tents throughout the feeding period. The other group ("non-tent-builders") are all of those species whose larvae construct tents after the feed-

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Fig. 1.—Plastic ice cream container with four *Megathymus ursus* larvae reared on artificial diet in PVC pipe sections. Scale in inches.

Fig. 2.—Closeup view of rolled paper tents shown in Fig. 1. from which *ursus* larvae have constructed silken tents. Dark particles adhering to tents are frass pellets. Scale in inches.

ing period and just prior to pupation. The latter group includes *Megathymus cofaqui* (Strecker), *Megathymus harrisi* Freeman, *Megathymus texanus texanus* B. & McD., *Megathymus texanus leussleri* Holland and *Megathymus streckeri* (Skinner).

The larvae of both groups present unique problems to rearing on artificial diet based mainly upon behavioral patterns. The basic problems, however, are 1) diet acceptance and establishment, 2) containment of the diet and larvae, 3) confinement of the larvae, and 4) replenishment of the diet and/or transfer of the larvae to fresh diet. The techniques developed and discussed herein have proven quite adequate for rearing scores of *Megathymus* larvae under completely artificial conditions. Larvae just newly-hatched, or field-collected in various instars, have been established on diet and successfully reared to adults in the laboratory utilizing these techniques.

Introduction and acceptance of artificial diet by *Megathymus* larvae is easily accomplished by the insertion of a small plug of yucca pulp into the diet. The yucca used is the native foodplant species of each *Megathymus* taxon being reared. One small (40 mm in diameter by 10 cm in length) yucca caudex will produce hundreds of plugs, and the unused portion of caudex may be stored in a household refrigerator for several months if properly sealed in plastic wrapping (freezer wrap).

TENT-BUILDERS

Containment of the diet differs for both larval groups. For the tent-builders, the author uses sections of Polyvinylchloride (PVC) irrigation pipe 24 mm in inside diameter by 80 mm in length which have been filled with diet. One end of the pipe is capped with a square of sheet aluminum 27 mm on a side by 0.5 mm in thickness which is taped to the pipe. The other end of the pipe is capped with a square of clear plastic sheet of approximately the same dimensions. In the center of each plastic square, a small hole is cut for the insertion of an artificial tent of rolled paper. The paper tent is pushed into the diet so that it surrounds the yucca plug inserted earlier. Then an ovum, still attached to a portion of the yucca leaf, is placed into the paper tent to await hatching, or, a larva in any instar is allowed to make its way into the tent and establish itself. Containers of this type, properly labeled, are placed upright in various small boxes, plastic bowls, etc., and maintained at room temperature. Larval transfers are easily accomplished and later, as the larvae mature, only a wrapping of polyethylene plastic is used to

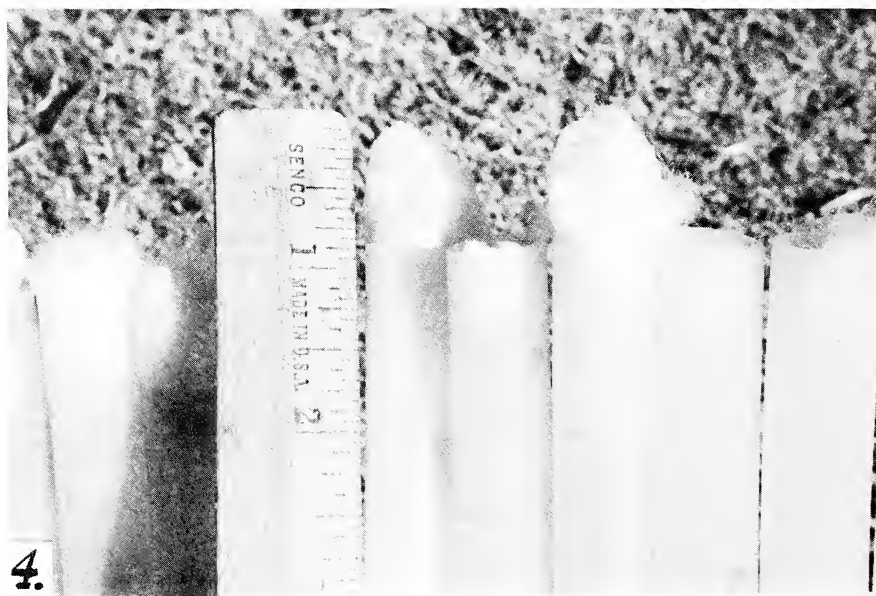


Fig. 3.—Metal tray container holding several *Megathymus streckeri* and *Megathymus texanus texanus* larvae reared on artificial diet in plastic tubes. Scale in inches.

Fig. 4.—Closeup view of plastic tube ends shown in Fig. 3. with two short tents made by *streckeri* larvae. Note that the cotton plugs have been incorporated into the tents. Scale in inches.

encase the PVC pipe ends in order to reduce moisture loss of the diet through evaporation. In some instances, a few larvae may begin to bore out of the bottoms of the pipes through the plastic wrapping. If the pipes have been set upon metal or tough plastic containers, further boring out is prevented. Tent-building larvae will defecate outside of the tent and the fecal pellets will accumulate on the bottoms of the boxes, etc. Mature larvae will powder up and pupate in their surrogate yucca caudices (pipes) after several months of feeding. Under laboratory conditions, the feeding period is markedly shortened and diapause may be non-existent or brief (lasting a few weeks instead of months).

NON-TENT-BUILDERS

For the non-tent-builders, the problems of rearing are more acute. Containers must be impenetrable to larval mandibles. In the early instars (up through fourth instar), the larvae of *streckeri* and *texanus* are notorious borers and must be confined at all costs. Otherwise, they may bore out unnoticed and escape, never to be found again, or discovered many days or weeks later in a state of severe desiccation.

Virtually all of the non-tent-building larvae reared by the author have been ex ova. The initial container is an ordinary plastic drinking straw filled with diet to within 20 mm of one end. The end of the straw destined to be the bottom is folded over and stapled down. The other end of the straw receives a small yucca plug which is pushed into the diet a short distance. Then an ovum, still attached to a portion of a yucca leaf, is introduced into the straw and the straw end folded over and stapled. The newly-hatched larvae will bore into the yucca plugs and ultimately into the diet. The straws, in clusters of twenty or more, are stood upright in ordinary glass jelly jars which have been properly labeled. As the larvae feed on the diet and moult, they are observed through the clear plastic. Frass is packed into the straws behind them. Before their diet is all consumed, the larvae may have outgrown the straws and will need to be transferred.

The next container is an intermediate one and consists of a semi-transparent polyethylene plastic tube 9 mm in inside diameter by 30.5 cm in length with a wall thickness of approximately 2 mm. This size will allow *streckeri* and *texanus* larvae to feed up through the fifth instar. The tube is filled with diet to within 4 cm of one end. At this end the larva is allowed to

make its own way in. Both ends of the tube are then capped with squares of sheet aluminum 10 mm on a side by 0.5 mm in thickness taped in place. The aluminum prevents boring out and escape of the larva. Sufficient air is present in the diet and the tube to allow for larval respiration. The larva is easily observed through the semi-transparent plastic. Ecdysis is accurately determined and exuviae readily recovered utilizing plastic tube containers.

The final container is similar to the intermediate one, the only difference being one of greater inside diameter. In this case, tubes measuring 12 mm in inside diameter are used. Larvae well into fifth instar and beyond will still require that aluminum caps be placed over the bottom ends of the tubes. The upper ends (tubes are placed upright or with one end higher than the other in various containers) however, from which the larvae will construct their tents, are plugged only with wads of cotton. The larvae will defecate against the cotton plugs. Later, after diapause, they will push out the cotton plugs or bore through them when tent building is initiated.

At any time during the rearing, it may become necessary to transfer the larvae to fresh diet. For non-tent-builders, removal of each larva is a simple matter. First, uncap both ends of the tube. Second, hold the tube so that the bottom end is above a level surface a few centimeters. Then, blow into the upper end of the tube with gentle but sustained pressure. This will force the contents of the tube (including larva) out of the bottom end and onto the surface. Thereupon, the larva may be collected, inspected and introduced to a new container.

The ideal container for a non-tent-building larva appears to be one in which the inside diameter of the tube corresponds exactly to the larval one. Non-tent-building larvae are notoriously wasteful if given a column of diet greater than their larval diameter.

The habit of plugging the burrow behind them with frass as they feed (in contrast to the tent-builders) exposes the non-tent-builders to the hazards of fungus and bacteria which may culture within the tubes. Aside from vigilance and transfer to fresh diet when this problem arises, the author has not found a satisfactory solution. Consequently, losses due to disease are much greater with laboratory reared non-tent-building larvae than with the tent-builders.

CONCLUSION

The use of artificial diet for the rearing of *Megathymus* larvae affords an opportunity to other workers interested in this genus. Under controlled laboratory conditions, resources permitting, there appears to be little limitation to the number of larvae or taxa involved which one can successfully rear to adults. Larval duration can be significantly reduced (depending upon the taxon) from a time span of around ten months to as little as 120 days from egg to adult by employing the techniques described herein.

It is hoped that the techniques presented in this paper will encourage others in the rearing of *Megathymus* larvae. Those who will try their hand at rearing these fascinating beasts are urged to try other techniques. By taking advantage of their innate larval behavior, the worker will find *Megathymus* larvae relatively simple to rear.

ACKNOWLEDGEMENTS

The author is deeply indebted to Mr. Merrill Petterson, USDA Vegetable Insects, Mesa, Arizona, for providing artificial diet as needed throughout these rearings.

The special efforts of Don B. and Viola Stallings resulted in additional ova of *streckeri* and *texanus* being made available for this study and to them the author is ever grateful.

Joseph R. Wielgus of Glendale, Arizona, provided pleasant companionship during fieldwork in 1974 and assisted in the rearing program.

Thanks are again due Dr. Frank F. Hasbrouck, Associate Professor of Zoology and Curator of Insects, Arizona State University, Tempe, Arizona, who critically reviewed the manuscript.

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BUTTERFLIES OF THE WORLD, by H. L. Lewis, illustrations by Lionel Leventhal Ltd. 1973. xvi + 312 p., 208 color plates, 2 drawings, 1 map. Follett Publishing Co., Chicago. Price \$29.95.

There has long been a need for a general butterfly book which covers a broad geographic area. Mr. Lewis's book accomplishes this admirably, as the coverage includes all families of butterflies on a world-wide basis. More than 5,000 species of butterflies are represented in the color plates. The author has made the following geographic divisions: North America, South America including Mexico, Europe, Africa, Asia, Indo-Australia. For each region, he has figured representatives of each family including the Hesperioidea, which are all too often excluded from major works. The more common species from each region are figured along with many of the uncommon ones.

The book will be valuable to the amateur and serious collector alike. Its major value will be enabling the easy identification of an unknown specimen as to family, and in most cases, genus, if the specimen itself is not figured. At this point, one can refer to the existing regional works for in-depth study.

Considering the relatively low cost of the book and the number of color plates, the plates are of excellent quality. Some plates are slightly off in color, but on the whole, they are very good. Each plate contains a small map of the geographic area represented. This is a nice touch and provides a convenient reference.

The text portion of the work is not really a scientific treatise. It presents information about some but not all of the specimens shown in each of the plates. This includes scientific name, authority, English name in some instances, general geographic distribution, similar species, brood information, and larval foodplant in some cases. There is included a complete index. The book is in reality a pictorial encyclopedia of the world's butterflies.

Mr. Lewis is to be complimented on his choice of the species figured. The treatment is well-balanced for each geographic region. He has not restricted the figures to "showy" species and the plates present a good general coverage of fauna.

As with any work of this scope, there are some negative comments to be made about the book. The author should have had his manuscript reviewed by collectors or authorities familiar with each of the geographic regions. There are some problems with nomenclature and misidentification of species and genera.

In the treatment of North American families, there is no consistency concerning the use of generic and subgeneric names, or in the use of species and subspecies names. Examples are the use of *Strymon* without recognition of *Chlorostrymon*, *Euristrymon* etc., while *Icaricia*, *Agriades* etc. are used rather than *Plebejus*. There are many instances of this nature. In plate 15, for example, *Speyeria calgariana* and *S. callippe* are figured without any indication that two subspecies of the same species are involved. This is a common occurrence throughout the plates.

A "corrigenda" sheet accompanied the book, but a number of items are not included. Some specific examples are:

Pl. 12. *Papilio daunus* is used rather than *P. multicaudata*; *Dione* rather than *Agraulis* is used; the butterfly figured (Fig. 17) as *Libytheana carinenta* appears to be *L. bachmanii larvata* (Strecker). Both *L. carinenta* and *Danaus eresimus* (Fig. 18) should probably be considered casual for the geographic region (North America exclusive of Mexico) presented. No mention of this is made in the associated text.

Pl. 13. *Anartia amathea* (Fig. 3) is not found in the region designated as North America by the author according to the map on page x.

Pl. 14. The genus *Metamorpha* rather than *Siproeta* is used. Fig. 25. *Polygonia orcas* is presumably *oreas*.

Pl. 15. *Thessalia leanira* is shown as *Phyciodes leanira*. *Speyeria adiante* rather than *S. adiate* is used. There is some question about including the Hawaiian *Pyrameis tammeamea* (Fig. 3) in the region represented.

Pl. 16. As in Pl. 15, species and subspecies names of *Speyeria* appear randomly. *Vanessa carye* is used rather than *V. or Cynthia anabella*.

Pl. 17. The insect figured (Fig. 17) as *Colias hageni* is *Colias interior*. The former is a ssp. of *C. philodice*. Fig. 18 appears to depict the underside of *Colias scudderii* and not *C. interior*. Fig. 19, is *Colias eurytheme* and not *C. pelidne*. There is confusion between *Anthocharis* and *Euchloe* as the generic name in several cases. *Paramidea* is introduced as the generic name for *Anthocharis genutia*, and *Pontieuchloia* for the genus in *P. protodice*. *Neophasia terlootii* is misspelled as *N. terlooi*.

Pl. 18. Fig. 15. *Gnodia portlandia* in place of *Lethe portlandia*. Fig. 16. *E. cymele* should be *E. cymela*.

Pl. 19. Fig. 6. *Satyrodes eurydice* is used rather than *Lethe eurydice*.

Pl. 19. *Plebejus (Icaricia) shasta* (Fig. 37) is assigned to *Lycaeides*. *Paramecera xicaque*, if from Arizona, should be *P. allyni*, (Fig. 6). Two extinct examples are shown in *G. xerces* and *G. x. fm. antiacis*.

Pl. 20. Fig. 12. *Glauconpsyche piasus daunia* is shown as *Phaedrotus* [sic] *sagittigera*. The associated text restricts the butterfly to the Rocky Mts. without mention of the coastal races. Fig. 17, *Plebejus aquila* [sic] = *aquilo*. Here *Plebejus* is used for *aquilo* when in Pl. 19, *Agriades* was used with *podarce*. The generic names *Lephelisca* and *Lymnas* are used rather than *Calephelis* and *Melanis*. All of the *Strymoniti* are treated as genus *Strymon*. *Strymon saepium* is shown as *Mitoura saepium*.

Pl. 22. *Hesperia ruricola* (Fig. 8) appears which is a *Nomen dubium*. Fig. 23, *Pholisora aepheus* [sic] = *P. alpheus*. Fig. 44, *S. zampa* = *pulverulenta* and the specimen shown is probably *S. evansi*. Fig. 25, *P. mejicanus*. The associated text states Canada to Texas for the range. Obviously *P. catullus* and *P. mejicanus* have been confused. The former is found from Canada to Mexico. The latter occurs in Colorado, New Mexico, Texas, and Mexico.

Pl. 24. Fig. 7, depicts a *Troides* as *Papilio xanticles*. The butterfly shown appears to be *Troides rhadamantus* (Lucas) from the Philippines. A similar confusion occurs on Pl. 136 as noted in the "corrigenda".

Pl. 43. Fig. 27. *Dryadula phaelusa* [sic] = *D. phaetusa*.

Pl. 48. Figs. 10, 11 *Lycorea ceres* and *L. cleobaea* appear to be misidentified.

Pl. 74. The genus *Lymnas* rather than *Melanis* is used.

This reviewer has restricted the majority of his critical comments to the North American region, the area with which he is most familiar. In the text which accompanies Plates 12-22, many of the listed geographic ranges are either incomplete or incorrect. A few examples have been noted above. This is truly unfortunate when such works as Klotz's *A FIELD GUIDE TO THE BUTTERFLIES* (1951), Ehrlich and Ehrlich's *HOW TO KNOW THE BUTTERFLIES* (1961), and many regional guides published in the past decade are available. The dos Passos Checklist has been available since 1964 for nomenclature, and several revisions have appeared. These shortcomings of Mr. Lewis's work detract from its overall quality and utility.

In some cases, European generic names have been applied to North American genera. It is not yet clear that these names correctly apply to our fauna.

Despite these failings, the book is still a useful reference, and one that many collectors will wish to own.

Clifford D. Ferris, Bioengineering Program, University of Wyoming, Laramie, Wyoming 82071.

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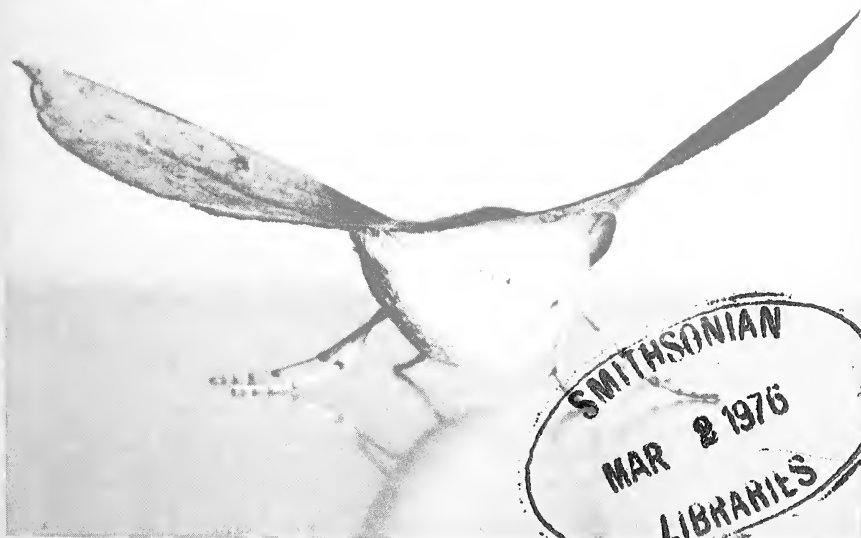
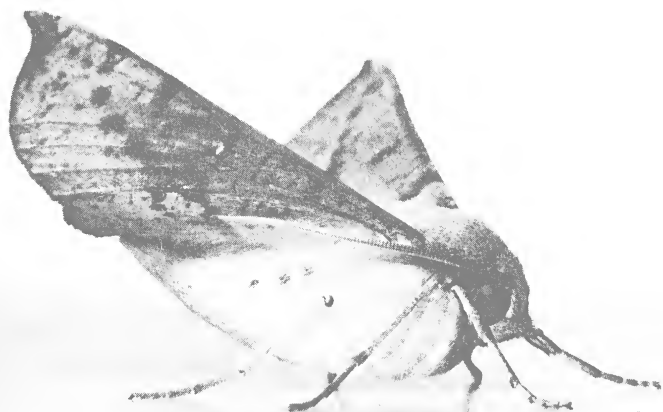
Number 4

December, 1974

IN THIS ISSUE

- | | | |
|--|--|-----|
| Toward a theory of butterfly migration | Oakley Shields | 217 |
| <i>Atrytonopsis hianna</i> biology and life
history in the Ozarks | J. Richard and Roger L. Heitzman | 239 |
| Larval migration of <i>Hyles lineata</i> (Fab.) | James F. Wells and Richard M. Brown | 246 |
| New food plant for <i>Darapsa pholus</i> (Cramer) | J. C. E. Riotte | 247 |
| Notes on Arctic and Subarctic collecting | Clifford D. Ferris | 249 |
| Kloet and Hincks' Check list of British Lepidoptera
Insects (Lepidoptera) Edn. 2. A reply to criticisms | J. D. Bradley, D. S. Fletcher and P. E. S. Whalley | 265 |
| The Nomenclature in an Important British
check list (1972). Part 3. Correct gender
for generic names derived from classical
without change of termination | Juraj Paclt | 267 |
| Artificial Diet: The key to the mass
rearing of <i>Megathymus</i> larvae | Ronald S. Wielgus | 271 |
| Review: Butterflies of the World
by H. L. Lewis | Clifford D. Ferris | 278 |

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MATE-LOCATING BEHAVIOR OF WESTERN NORTH AMERICAN BUTTERFLIES

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Abstract. Mate-locating behavior, including the methods used to locate mates, the location of mating in relation to the larval foodplants and to topography, and the time of day of mating, was studied in 284 species of western north american butterflies and skippers. 18 pairs of congeneric species of butterflies and skippers were found to mate at contrasting topographic sites; the use of separate mating sites by these congeneric species certainly prevents, and may result from, interference competition during mate-locating behavior. Some trends in mate-locating behavior were observed: 1) perching species more often tend to mate in restricted sites in the habitat, and more often mate during a restricted part of the day, than do patrolling species; 2) perching rather than patrolling behavior is more frequent in species that have only 1-2 rather than 3-4 broods; 3) species emerging at the end rather than at the start of the season, and species with large movements, more often have patrolling rather than perching behavior and more often mate throughout the habitat rather than in restricted sites; 4) species feeding on shrubs or trees rather than on herbs more often tend to be perching rather than patrolling species and more often tend to mate during a restricted part of the day; 5) high mountain species usually patrol and mate at any time of day. Mate-locating behavior provides many useful taxonomic characters; closely related species usually have similar mate-locating behavior. Despite the trends noted above, different mate-locating strategies are often used by species feeding on the same larval foodplants. The strategy used often seems to be that used by a taxonomic relative feeding on other plants, but convergence of mate-locating behavior of taxonomically distant species feeding on the same plants has sometimes occurred.

MATE-LOCATING BEHAVIOR IS DEFINED as behavior which brings the sexes together for mating. It includes the methods used to find mates, the location of mating, and time of day of initiation of mating (Scott, 1974a).

Elsewhere I presented a general discussion of mate-locating behavior of butterflies (Scott, 1974a). There are three methods used to locate mates: *perching behavior* (males rest at characteristic sites and investigate passing objects by flying out at them to search for females; females generally fly to these sites to mate, then they depart), *patrolling behavior* (males fly almost continuously in search of females), and use of pheromones from more than a few meters away (this method seems quite rare).

Movement, size, wing color, wing pattern, and odor are stimuli which can be transmitted during sexual communication in the approach of a male to a female (Scott, 1973a). Perching males are highly attracted to moving objects, whereas patrolling males often are attracted to motionless objects resembling in some way females. A patrolling male may rarely find a female which gives off a pheromone when he wanders near her position. Perching species usually mate in limited areas of the habitat, often during only part of the day, whereas patrolling species usually mate throughout the habitat at any time of day.

This paper is a detailed survey of mate-locating behavior of several hundred western North American butterflies (Papilionoidea and Hesperioidea). In it I summarize mate-locating behavior for each species, and attempt in the discussion to determine major trends of behavior among all the species.

METHODS

To determine mate-locating behavior, adult behavior was observed, especially interactions between males and between sexes (including courtship and mating). In perching species, such interactions occurred predominantly when resting males investigated moving objects. In patrolling species, interactions occurred predominantly when resting males investigated moving objects. In patrolling species, interactions occurred predominantly when flying males investigated either flying or resting individuals. Perching and patrolling differ from resting and flying respectively, by the addition of investigative behavior. In a few species, noted in the results, both behavior patterns occur.

Location and time of day of mating were determined from field observations of such interactions. Varied topographic and vegetational sites were studied when possible to make sure that a restricted location of mating was characteristic of the population rather than due to limited opportunity.

Time of day of mating in this paper refers to initiation of mating. Therefore, field observations of copulating pairs were used with caution when initiation of mating was not seen. This is because copulation occasionally lasts several hours (very rarely several days) (Scott, 1973a), so that time of observation of the pair lags behind time of initiation. It is therefore possible to observe a copulating pair in the afternoon, if in that species courtship only occurs in the morning. Therefore time of day of mate-locating behavior, courtship and initiation of mating, were

given priority over time of observation of copulating pairs whose initiation was not seen. Species which are stated herein to court and mate during only part of the day were carefully studied to make sure that the restricted mating period was characteristic of the population and not a result of inclement or unusual weather.

The ideal method of studying the mate-locating behavior is to observe and record all details of male-male and male-female interactions, including dozens of completed courtships. For some species in this paper such as *Precis coenia* the data are based on more than 40 completed courtships in addition to other courtships and male behavior. However, it is not necessary to observe many completed courtships to determine mate-locating behavior. In all the species so far studied in detail (see literature cited), the following statements are true. In butterflies, the mating process always involves an investigation by the male of other individuals. Mating therefore occurs only at the locations where males investigate other individuals, and only during the time of day when males investigate other individuals. The method of mate-location is determined by observing whether males fly or sit before interacting with other individuals. These statements suggest that a complete description of mate-locating behavior can therefore be based only on male behavior, but observations of completed courtship are desirable supplements for confirmation. I include some species in this paper for which no completed courtships were seen.

Study of mate-locating behavior of butterflies can easily be carried out by those readers willing to spend field time observing behavior. The basic method is to observe interactions (male-male and male-female) and to record when and where these occur, and whether the male was resting or flying just prior to the interaction. Observations of resting or flying alone are of very little value without observations of interactions. Again I emphasize that perching and patrolling as I define them differ from resting and flying respectively in that perching and patrolling males investigate other individuals, whereas resting and flying males may not. I emphasize this because some people are treating the words perching and patrolling as the same as resting and flying respectively; to avoid such confusion it may eventually be necessary to propose special latin names for perching and patrolling behavior.

Some authors would use territoriality prominently in a discussion of mate-locating behavior. Territoriality may be defined

as males remaining in a small area to search for females, where males intentionally drive away other males. It may therefore be the fourth criterion for classification of mate-locating behavior (the first three being where mating occurs, when it occurs during the day, and the method used to locate females (perching or patrolling usually)). I do not use "territoriality" because no butterfly has conclusively been shown to be territorial with my interpretation of the vertebrate definition of territoriality (Scott, 1974a), and because demonstration of territoriality requires detailed study of movement of marked individuals which are beyond the scope of this paper. Some previous authors have used "territoriality" for what I call perching behavior, other authors have used it for what I call patrolling behavior where males sometimes return to the same spot, and still other authors apparently do not use it in any consistent manner. The methods and terms used in this paper were operationally constructed for use with butterflies, whereas "territoriality" was originally used for vertebrates and has since been applied so loosely that its meaning has become diffuse and the benefits from its use (especially with invertebrates) have become few.

RESULTS

These studies were conducted mainly in Colorado, especially the eastern slope of the continental divide and adjacent plains, and to a lesser extent in other western North American states and provinces, especially California. Eleven species were studied in detail in Colorado and California from 1969 to 1973 (see literature cited). During 1972 to 1974 over 200 field days were spent, mainly in Colorado, gathering data for this paper.

Supporting data including localities and times of observations of interactions, courtship and mating are not included in this paper due to space limitations; these data can be obtained from the author should they prove important to the reader. As a compromise I have indicated the quality of the observations as follows (a—about 100 or more observations of interactions, conclusions unlikely to change with further study; b—about 50-100 observations of interactions, conclusions may change slightly with detailed study; c—less than 50 observations of interactions, conclusions may change somewhat with further study and are presented mainly to increase the taxonomic variety studied). Localities studied are the eastern slope of the continental divide and adjacent plains of Colorado (Jefferson, Boulder, Douglas, El Paso, Clear Creek, Park, Chaffee, Custer, Pueblo, Fremont,

and Saguache Counties) unless otherwise stated. An asterisk is used for species occurring in the Pueblo area (Pueblo, Fremont, Custer, Chaffee, Huerfano, and Saguache Counties, Colorado) because these are analyzed in the discussion. Shields & Emmel (1973) have also compiled a list of mating times, and Shields (1967) provides information on several species not mentioned here. Several errors in Table 2 of Scott (1974a) are corrected herein. All times are reported as 24-hour standard time. The words "all day" in any context mean that interactions occurred at least from before 0900 to after 1500.

PAPILIONIDAE

Parnassius clodius. Males patrol all day about meadows and hillsides near the larval host. They patrol most often in swales, and often dip down between shrubs to search there; males have a somewhat bobbing flight (Nevada, El Dorado, and Siskiyou Cos. Calif.—b).

**Parnassius phoebus*. Males patrol all day in open areas where the larval host is abundant, slightly more frequently in sheltered sites (Scott, 1973b). Patrolling is most frequent on the leeward side of ridges both in Colorado and in California (Alpine & Siskiyou Cos.). Males patrol about $\frac{1}{2}$ m above ground, with a faster and steadier flight than *P. clodius* (a).

**Papilio polyxenes*, **P. bairdii*, **P. zelicaon* (and form *nitra*). Males patrol and sometimes perch, throughout the day (about 0900-1530 for Colorado *zelicaon*). At the usual fairly low density, males patrol but often perch, mainly on large hilltops. At high density and in the absence of hilltops males patrol and mate near the larval hosts (Guppy, 1969). In riparian forest, males perch in clearings among the trees (Sacramento, California, Arthur Shapiro, pers. comm.). Some hilltopping males in some localities may patrol only in a restricted area of a hilltop; this behavior might possibly be territorial (a).

Papilio indra. Males perch and patrol all day at about equal frequency, on somewhat sheltered rocky outcrops just below a hilltop (Jefferson Co. Colo. & Napa Co. Calif.) (b).

**Papilio rutulus*. Males patrol all day up and down streams with much riparian vegetation (they rarely patrol on hilltops for a few minutes in Colorado and Napa Co. Calif., then depart). In Davis, California, a suburb, males patrol about sunlit openings in wooded parts of the city (b).

**Papilio multicaudata*. Males patrol all day up and down canyon bottoms, which are usually drier than those frequented

by *P. rutulus* (a).

Papilio eurymedon. Males patrol (and sometimes perch) all day on large hilltops; males often patrol a small area there (Colorado, Napa Co. Calif.) (b).

Battus philenor. Males patrol all day on hillsides and flats near the larval host in Contra Costa and Yolo Co. California (they occasionally patrol on hilltops near Austin Texas and in Napa Co. California) (c).

PIERIDAE

**Anthocaris sara*. Males patrol all day up and down valley bottoms, or more haphazardly on flat land, but always near trees in forested areas (b).

Anthocaris lanceolata. Males patrol all day mainly in valley bottoms or steep hillside draws (El Dorado & Nevada Cos. Calif.) (c).

A. cethura. Males patrol on windless sides of ridgetops at least from 1130-1430 (Churchill Co. Nevada) (c).

**Euchloe ausonides*. Males patrol all day in open areas, slightly more frequently in valley bottoms than elsewhere, in Colorado and Contra Costa Co. Calif. (a; Scott, 1975a).

**E. olympia*. Males patrol all day on hilltops (b).

E. hyantis. Males patrol all day usually on hilltops, but sometimes throughout the habitat or restricted to areas of larval foodplant (Napa & Nevada Cos. Calif., Churchill & Lander Cos. Nevada, Pima Co. Arizona) (b).

**Colias meadi*, **alexandra*, **eurytheme*, **philodice*. Males patrol all day in open areas regardless of topography. (b).

C. occidentalis. Males patrol all day in valley bottoms, open woods, or on hillsides near the larval host (Colusa & Lake Cos. Calif.) (c).

C. cesonia. Males patrol all day, especially in valley bottoms and on flats (Pima & Santa Cruz Cos. Arizona) (c).

Eurema nicippe, *mexicana*, *proterpia*, *boisduvaliana*. Males patrol all day, mainly in gullies and flats (Pima & Santa Cruz Cos. Arizona) (c).

**Nathalis iole*. Males patrol all day several cm. above ground, mostly in gullies, roadsides, or flat land (c).

**Pieris chlorodice beckeri*. Males patrol all day up and down usually dry arroyo bottoms (Colorado, and Churchill Co. Nevada; b).

**P. sisymbri*. Males patrol all day, usually on hilltops, haphazardly when on flat land (Colorado, and Napa, Colusa, &

Alpine Cos. Calif.) (a).

**P. callidice occidentalis*. Males patrol all day, mainly on hilltops when they are available (b).

**P. protodice*. Males patrol all day, often on hilltops, but often on flat land when hilltops are unavailable (b).

**P. napi*. Males patrol all day along partly shaded streams in forests. Except for *A. sara*, the other Pieridae prefer open areas (b).

**P. rapae*. Males patrol all day near larval hosts near riparian vegetation in native habitats and on flat land in cultivated areas. They share the slow patrolling flight of *P. napi* (b).

**Neophasia menapia*. Males patrol all day, circling slowly about the larval foodplant trees (b).

Phoebis sennae. Males patrol all day, often on flat land (Mexico and Texas).

NYMPHALIDAE

**Euptychia dorothea*. Males patrol all day up and down narrow dry shaded gullies (b).

E. rubricata. Males patrol all day, usually in semi-shaded sites such as gullies (Texas) (c).

Euptychia cymela. Males patrol all day, mainly in woods under shading trees (Ohio, and Yuma Co. Colo.) (c).

**Coenonympha tullia*. Males patrol all day in grassy areas regardless of topography (a).

**Neominois ridingsii*. Males perch (and seldom patrol briefly) from about 0750 to about 1100, strongly from 0830 to 1000, and rarely later in the day, on small (3m) grassy hilltops, mesas, or saddles (Fremont Co. Colo., Scott, 1973c). Behavior in Mono Co. Calif. is similar (a).

**Cercyonis pegala*. Males patrol all day in grassy areas, mainly around riparian trees (b).

**C. oetus*. Males patrol all day in open grassy areas regardless of topography (b).

C. sthenele. Males patrol all day in grassy areas, often in gullies and valley bottoms (California, Colorado) (c).

**C. meadi*. Males patrol all day everywhere in the habitat but most often in valley bottoms and in woods (b).

Oeneis nevadensis. Males perch all day on fallen trees and other objects in lanes of valley bottom forest (Siskiyou Co. Calif., c). Males also perch on hilltops, but I have not seen this.

**O. chryxus*. Males perch (and occasionally patrol briefly) all day, usually on hilltops or on sloping ridgetops (Colo.) (b).

O. c. ivallda males perch and when disturbed patrol before settling, all day on ridgetops (Inyo Co. Calif.).

**O. alberta*. Males perch, and often patrol 10 m or less, all day among bunch grasses, usually in somewhat sheltered hollows of hillsides and valley bottoms (c).

**O. uhleri*. Males perch, and occasionally patrol short distances, all day on slopes at the base of bunch-grass community, or on a trail below the bunch grass community, usually on south-facing slopes (b).

O. polixenes. Males mainly patrol but sometimes perch (patrolling flights are often 10 m or more) all day in swales on grassy north-facing slopes (b).

**O. melissa*. Males perch, and often patrol, all day in rocky areas of hilltops and ridgetops (b).

O. taygete. Males perch and patrol all day on grassy hillsides and sometimes on hilltops (b).

**Erebia magdalena*. Males patrol all day over rockslides (b).

**E. epipsodea*. Males patrol all day over wet grassy meadows or swales (b).

E. theano. Males patrol all day about grassy areas on slopes or in bogs; males appear to be very local and spend most of their time sitting among vegetation (Hinsdale Co. Colo., c).

E. callias. Males patrol all day usually over alpine cushion plant community, often over rounded ridges, but sometimes on slopes (b).

Gyrocheilus patrobas. Males patrol all day, usually in shady grassy areas in oak woodland (southern Arizona, c).

**Euptoieta claudia*. Males patrol all day in every topographic situation in open areas, especially on flats (b).

Speyeria nokomis. Males patrol all day in spring-fed meadows, especially in valley bottoms if the spring is on a slope. Males fly about $\frac{1}{2}$ m above ground and dip into hollows to search (Mono Co. Calif., Kane Co. Utah, Uinta Co. Utah, Mesa Co. Colo., b).

**S. aphrodite*. Males patrol all day, mainly in open areas, regardless of topography (a).

**S. edwardsii*. Males patrol all day in open areas regardless of topography, but several males patrolled in a small space just below the summit of a large hilltop, remaining there for several hours (b).

**S. coronis*. Males patrol all day in open areas regardless of topography (*S. aphrodite*, *edwardsii*, and *coronis* often patrol

the bottoms of valleys) (b).

S. zerene. Males patrol all day in open areas regardless of topography (Routt Co. Colo.; Idaho) (b).

S. callippe. Mate-locating behavior occurs all day. In the Front Range of Colorado, males patrol and occasionally perch on shrubs etc., mainly on hilltops until about 1300, when they patrol (very rarely perch) more generally on hillsides. Courtship and mating occur all day despite this behavioral switch. Males patrol in fairly open areas close to the ground, in contrast to the preceding four species of *Speyeria* which patrol about 1 m above ground (b). In Glenn and El Dorado Counties, California, males patrol all day about $\frac{1}{2}$ m above ground in the flat forest (c). At Mt. Diablo, Contra Costa Co. Calif., males sometimes perch on shrubs, grass, etc., and also patrol. Perching was noticed sometimes until about 1200, after when males would only patrol. Perching and patrolling occurred only on the upper 100 feet of the hilltop, mostly in clearings on the ridge (c).

S. atlantis. Males patrol all day in wet meadows and along streams in Colorado (b) and Coconino Co. Arizona, and patrol about open forest all day in Glenn Co. Calif. (c).

S. egleis. Males patrol all day, mostly along shaded forest lanes such as abandoned roads, about $\frac{1}{3}$ m above ground (Routt Co. Colo., b). In Mendocino and Alpine Cos. California, males patrol all day near the ground mostly on hilltops (c).

**S. mormonia*. Males patrol all day just above the ground in open vegetated areas regardless of topography, usually in meadows at lower elevations (b).

**Boloria selene*. Males patrol all day in wet meadows and springs, usually on fairly level land but sometimes on hillsides (b).

B. eunomia. Males patrol all day among the willows of willow bogs, often near the edge of a bog. (b).

B. frigga. Males patrol all day, in willow bogs, usually in low spots between a slope and a flat, in mixed willow-grass parts of the willow bog (but some males can be found throughout the bog) (b).

**B. freija*. Males patrol all day in open areas near the larval hosts, usually at the edge of a bog or stream, often on hillsides (b).

**B. titania*. Males patrol all day in open areas, usually swales and valley bottoms, in meadows or bogs. At willow bog localities, males patrol the borders of the bog but rarely enter the bog

center (b).

B. toddi. Males patrol all day in moist meadows (Alberta, Summit Co. Colo.) (c).

B. epithore. Males patrol all day in moist shrubby meadows and moist open woods, primarily in valley bottoms (Siskiyou & Glenn Cos. Calif., b).

B. alberta. Males patrol all day over open nearly barren or vegetated flats and hillside scree slopes, especially where *Dryas octopetala* is abundant (Alberta, c).

B. astarte. Males patrol all day on ridgetops and hilltops, usually just below the leeward edge of the ridgetop or plateau (Alberta, c).

B. kriemhild. Males patrol, at least during morning and mid-day, over moist meadows, usually where aspen is common (Montana, c).

**Euphydryas chalcedona*. Males perch and occasionally patrol all day. Perching often occurs on shrubs in hollows below a slope (Napa Co. Calif., b). Near Rosita, Custer Co., Colo. (*E. c.* near *eurytion*), males patrol all day in meadows, especially in grassy swales (b). At Aspen, Pitkin Co. Colo., males patrol all day all over a hill (c). In the foothills of the Colorado Front Range (*E. c. capella*), males usually perch but sometimes patrol, all day on low and large hilltops (c). At Diamond Peak, Moffat Co. Colo. (*E. c.* near *bernadetta*), behavior is very similar to *capella* (c). In Sevier Co. Utah, males patrol as in *eurytion* (c). In El Dorado and Alpine Cos. Calif. (b), *E. c. sierra* males patrol and sometimes perch all day on hilltops at low density, but mainly patrol throughout the habitat especially over flowers at high density.

Euphydryas editha. In western Colorado (Moffat Co. and Pitkin Co., b) males patrol and often perch all day on ridgetops and hilltops. At Connors Pass, White Pine Co. Nevada (c), males mainly perch on hilltops. At Jasper Ridge, San Mateo Co. Calif., males only patrol all day (Labine, 1966). At Butts Canyon, Napa Co. Calif. (c) males perch and patrol about equally on ridgetops all day. At Blue Ravine, Sierra Co. Calif. (c), males patrol and sometimes perch on shrubs on a serpentine slope. At Goat Mtn., Colusa Co., Calif. (c) behavior is similar but is on a ridgetop. At Mono Pass, Inyo Co. Calif. (c), males patrol and sometimes perch all day on a ridgetop.

**Poladryas minuta*. Males perch and rarely patrol on ridgetops and hilltops from about 0700 to 1230; from about 1230 to

about 1500 males patrol, usually on hillsides and flats etc. near flowers. Courtship occurs throughout the day (a; Scott, 1974).

Chlosyne palla. In Gilpin and Routt Cos. Colorado (b), males perch, and sometimes patrol, all day, on slight prominences such as mine dumps in a valley bottom or on the outer edge of a dirt road rounding a hillside. In El Dorado County Calif. (c) males patrol and perch about equally, usually in valley bottoms, roadside ditches, or swales, all day. Males patrolled near flowers on a ridgetop once in Napa Co. Calif. (c).

Chlosyne definita. Males patrol just above the ground all day, all over the ridgetops, hillsides, and gulches where a population occurs (western Texas, b).

Chlosyne chinatiensis. Males patrol all day just above the ground, mainly on ridgetops where *Agave lecheguilla* is abundant; colonies may be somewhat local, being scarce on a ridge and common on an adjacent ridge (western Texas, c).

Chlosyne theona. Males patrol all day on flats mostly (Mexico, c). In southwest Texas and central Arizona males often occur on hilltops, however (c).

Chlosyne neumoegeni. Males perch, and sometimes patrol, in gulch bottoms (like *Phyciodes mylitta*) at least from 1130 to 1440 when observations were made (Pima Co. Ariz., c). In San Bernardino Co. Calif. males perch in gulch bottoms all day (c).

Chlosyne hoffmanni. Males patrol all day about $\frac{1}{2}$ m above ground about valley bottom meadows, swales, and adjacent shrubland near the larval host (Siskiyou Co. Calif., c), and in roadside ditches (El Dorado Co. Calif., c).

**Chlosyne acastus*. Males perch, and sometimes patrol, in dry washes and gullies all day (Fremont Co. Colorado, southern Utah, b).

**Chlosyne damoetus*. Males patrol all day over rockslides where the larval host is abundant (Custer Co. Colo., c). In Alberta and California (Tuolumne, Mono, and Alpine Counties) behavior is similar but males often patrol up and down chutes in the rockslide (c).

**Chlosyne leanira fulvia*. Males court and mate all day. At fairly low density, males perch and occasionally patrol on low hilltops near the larval host. Several times high density was encountered, and males patrolled and mated in a relatively small area where the population was concentrated (b). *C. l. alma* males perch, and sometimes patrol some after an encounter, on hilltops (Kern Co. Calif., c). *C. l. leanira* males mainly perch

and sometimes patrol on hilltops all day (Napa Co. Calif., c).

Chlosyne elada. Males patrol all day about $\frac{1}{2}$ m above the ground throughout the habitat, often on flats (Arizona, Texas, Mexico, c).

**Chlosyne gorgone*. Courtship and mating occur all day. On hilltops, males mainly perch and seldom patrol. On hillsides and valleys, males almost always patrol (b).

**Chlosyne nycteis*. Males patrol all day along streamsides near *Rudbeckia laciniata* (b).

Chlosyne lacinia. Courtship and mating occur all day. Like *C. gorgone*, males patrol and sometimes perch on hilltops in Texas, but elsewhere they mostly patrol (Mexico) (c).

**Phyciodes tharos*. Males patrol all day in wet meadows and streamsides (b).

**Phyciodes campestris*. Males patrol all day just above the ground, mostly in meadows, grassy swales and valley bottoms (Nevada & Yolo Co. California, and Colorado, a).

**Phyciodes picta*. Males patrol all day just above the ground in colonies mainly on flat land such as near streams, vacant fields, beside railroad tracks, etc. (b).

Phyciodes pallida. Courtship and mating occur all day. Males usually perch in gullies on 1 m tall twigs or other objects. At Red Rocks, Jefferson County, Colorado, most males perched in gullies but some males patrolled on slopes near a hilltop and rarely males are found on hilltops (b). At Connors Pass, White Pine County, Nevada, all three males observed patrolled on ridgetops.

Phyciodes mylitta. Mating occurs all day. In California and Arizona males usually perch in gullies or between riparian shrubs and a hillside (and occasionally patrol about $\frac{1}{3}$ m above ground, b). However, in agricultural areas of Idaho, Washington, and central California, males patrolled near *Cirsium arvense*, a larval host growing in waste places (b).

Phyciodes orseis. Males perch all day, and occasionally patrol, in gullies and between riparian shrubs and hillsides (Siskiyou Co. California, Douglas Co. Nevada; b).

Phyciodes phaon. Males patrol all day, mostly on flats near the larval hosts (western Texas, c).

Phyciodes vesta. Males patrol all day, often on flats, often near waterholes in arid areas (Texas, c).

Phyciodes texana. Males usually perch (and occasionally patrol about 1 m above ground), all day, mainly in gulches and

dry stream beds (southern Arizona, c).

Microtia dymas. Males patrol slowly all day, most often in gullies and flats in hilly areas (southern Arizona, western Texas; c).

Microtia elva. Males patrol slowly all day all over the habitat, although colonies are somewhat local (Mexico, c).

**Polygonia satyrus*. Males perch on vegetation in gullies or along tree-shaded banks, from about 1230 to late afternoon (b).

**Polygonia faunus* ("hylas"). Males perch on shrubs or rocks etc. in gullies, from roughly about 1300 to late afternoon (b). My observations on *Polygonia* and *Nymphalis*, especially *P. faunus*, indicate that hibernating individuals usually mate in spring.

**Polygonia zephyrus*. Males perch on bushes or stones, logs, etc. in valley bottoms, from roughly about 1230 to late afternoon (perching most actively after about 1300) (southern Colorado, and Douglas Co. Nevada) (a).

P. oreas. In California, males perch on shrubs and small trees in small clearings in valley bottoms (sometimes 3m above ground), at least in the afternoon when observations were made (c).

**Nymphalis antiopa*. Males perch, and occasionally patrol, in gullies or swales, and in valley bottoms, from about 1130 to at least 1700 (start of perching behavior is gradual) (b).

**N. californica*. Males perch, and occasionally patrol, starting about 1400 and perching until 1700 at least, especially on ridgetops, or on banks of valley bottoms, and on flat land on the side of trees, etc. (California, Colorado) (b).

**N. milberti*. Males perch usually behind shrubs on hilltops, sometimes on logs etc. next to gully banks. Males arrive between 1050 (rarely) and about 1400, averaging perhaps 1230, and then perch until late afternoon (b).

**Vanessa atalanta*. Males perch, usually on the leeward side of shrubs on hilltops, or on porch roofs of farm houses, and in similar situations (b).

**V. virginiensis*. Males perch, often on shrubs on hilltops, or on the leeward side of shrubs on flats (c).

**V. caryae*. Males perch, on shrubs on hilltops, or on flat land on the ground behind cars or people or other large objects (c) (Colorado and Yolo Co. Calif., c).

**V. cardui*. Males perch and sometimes patrol, usually on shrubs on hilltops at low density. All four *Vanessa* species first

arrive on hilltops at about 1330 plus or minus an hour or more depending on meteorological conditions (Shields, 1967), and most mating and courtship and perching occurs after this time until as late as 1930 in June. The situation is not this simple, however. In 1973 *V. cardui* was extremely abundant in Colorado. Numerous interactions between individuals were seen from 0800 onward, although intensity and frequency of interactions was greatest in afternoon especially late afternoon. Mrs. Betsy Webb of the Denver Museum of Natural History observed a complete courtship and mating at about 1200. Interactions occurred wherever individuals were, including hillsides (a).

Precis coenia. Males perch all day on flat bare spots in fields, trails, etc. (Scott, 1975b; a).

Adelpha bredowii. Males perch on 1-2 m shrubs usually in gulches, and sometimes patrol, all day (Napa Co. Calif.; c). Courtship occasionally occurred on Buckeye flowers.

**Limenitis weidemeyeri*. Males perch, and rarely patrol, all day in gullies and valley bottoms on bushes and treelimits about 2-3 m above ground (a).

L. lorquini. Males perch all day on shrubs about 2-3 m above ground (Siskiyou Co. Calif.) in valley bottoms (c).

**L. archippus*. Males patrol all day along willow groves along streams and irrigation ditches (b).

L. arthemis arizonensis. Males patrol all day along willow groves; rarely in Texas males patrol a small area of a hilltop (southern Arizona, western Texas; c).

**Asterocampa celtis*. Males perch on small trees along gullies, on the rocks and logs and other objects at the side of a gully, and often on my hat or net in a gully, or on the larval host trees on flat land. Males perch most actively from early afternoon to dusk, but interactions occur all day, as in *V. cardui*.

Asterocampa leilia. Males perch all day on rocks etc. in gully bottoms, although there may be a gradual change in activity as in *A. celtis* (s. Arizona, w. Texas; c).

**Anaea andria*. Males perch all day in clearings among cottonwood groves, on stones, logs, and branch tips up to 3 m above ground in the clearings (c).

**Danaus plexippus*. Males patrol in flat areas near the larval host, and interactions occur all day as early as 0800 (b, Colorado). Dr. Lincoln P. Brower (pers. comm.) has observed many matings all day in California, where mating occurs in early spring at the roosting sites. The preference of *D. gilippus* for mating in afternoon more than in morning may have been due to the warmer afternoon weather (Brower et al. 1965).

LYCAENIDAE

Calephelis arizonensis. Males perch all day in narrow gully bottoms, on plants about $\frac{1}{2}$ m above the gully bottom such as grass inflorescences (Santa Cruz Co. Ariz., c).

C. rawsoni freemani. Males perch all day on vegetation in narrow gullies, or at the side of broader gulches (Chisos Mts. Texas, c). Two other *Calephelis* spp., *C. nemesis* and *C. wrighti*, behave differently. They remain on or near the larval hosts (*Clematis* in southern Texas and *Bebbia juncea* near Blythe, California respectively), and occasionally perch and may also patrol there (c).

**Apodemia nais*. A population was studied in Custer Co. Colo. (b) in which individuals occurred on and near *Ceanothus* bushes. Males perched usually on 1/5 m tall dead stalks in open areas partly surrounded by shrubs between the mouth of the gulch and a roadside ditch, occasionally on the tip of a *Cercocarpus* shrub in a clearing at the mouth of the gulch. Perching behavior started almost precisely at 1130 in three days observations and lasted until about 1430. Before and after this perching period, and seldom during, males feed on *Ceanothus* flowers where females oviposit on *Ceanothus*.

**Apodemia mormo*. Males perch near the larval foodplant (*Eriogonum jamesi* in Chaffee County, Colo., where most observations were), mostly in depressions such as gullies cutting into hillisides, and depressions at bases of slopes. Perching starts about 1100 and continues til 1430 or later. In the morning males mainly feed on the larval host and fly away when disturbed.

**Hypaurotis crysalus*. Males patrol over and around tops of the larval host trees, starting (gradually) about 1400 and ending about 1730 (Scott, 1974d; a).

Atlides halesus. Males perch on treetops on hilltops, at least in the afternoon when observations were made (Arizona, New Mexico) (c).

**Strymon melinus*. Males perch on small trees on hilltops when available (on tall shrubs elsewhere) from about 1300 (roughly) to nearly dusk (b).

**Harkenclenus titus*. Males perch on small shrubs on hilltops (on taller shrubs if a colony occurs on flat land), from about 1000 (not earlier) to late afternoon. Mating sometimes occurs on the larval host (*Prunus virginiana*) (b).

**Satyrrium acadica*. Males perch (and seldom patrol) on

small willow or other plants about 1 m tall, especially on low plants growing out from a willow grove (up to 3-4 m away from the grove), from about 1350 to dusk (b).

Satyrium californica. Males perch (and occasionally patrol) on top of 2-6 m trees and shrubs on ridges and hilltops usually, from about 1400 to dusk (Jefferson Co. Colorado, and Napa Co. Calif., b). One courtship occurred on a Buckeye flower in California.

**Satyrium sylvinus*. Males perch (and seldom patrol) on small willow or other plants, especially those growing a few m out from a willow grove, from about 950 (not earlier) to late afternoon (about 1500) (Colorado, b). The same behavior was observed in Mono Co. California and Lander Co. Nevada in afternoon (c).

**Satyrium liparops*. Males perch on bushes or tree limbs about 1-2 m tall or less (sometimes on the side of a small tree) in gullies in the Front Range of Colorado (b). Perching and courting occur all day. In Routt Co. Colo. males perched on such shrubs on hilltops at least in morning (c).

**Satyrium calanus*. Males perch all day on small shrubs or other objects in gullies or depressions in oak groves in southern Colorado (b). In Routt County, Colo., however, males perched on small shrubs on hilltops at least in morning (c).

S. auretorum. Males perch and sometimes patrol on top of about 5 m tall oak trees on ridgetops and hilltops, mainly from about 1445 to dusk. Courtship sometimes occurs on Buckeye flowers. I noticed that *S. auretorum* and *S. californica* usually perched on separate trees (Napa Co. Calif., b).

S. tetra. Males perch on the *side* of shrubs and trees (commonly 1-2 m above ground on the shrub). They do this on hilltops (from about 1345 to dusk in Napa County, from about 900-1000 to dusk but mainly from 1230 onward in Contra Costa Co. Calif. (Mt. Diablo)), and they perch also on the side of tall shrubs on or near the larval host (*Cercocarpus betuloides*) in a valley bottom (late afternoon to dusk, Napa Co.). More work is needed on the time of day of mating; there seems to be a clear preference for late afternoon to dusk (b).

S. saepium. Males perch all day about 1 m above ground on small shrubs or halfway up larger ones on ridgetops and hilltops (Jefferson Co., Colorado, c; Contra Costa Co., Calif., c). In Colusa Co. Calif. males perched all day on the side of shrubs on the side facing the hillside, in addition to hilltops (c).

**S. behrii*. Males perch all day on top of shrubs or small trees on hilltops (b).

S. fuliginosum. Males usually sit on shrubs including the larval hostplant lupines, and every few minutes patrol erratically about the canopy of the lupines. They do this usually about shrubs in the lee of a ridgetop from at least 1130 to 1600 (Tuolumne and Alpine Cos. Calif., c).

**Callophrys spinetorum*. Males perch all day on top of prominent trees, especially on hilltops (Gilpin Co. Colo., Arizona; c).

**Callophrys nelsoni siva*. Males perch all day on top and sides of junipers, especially those on a ridge (often sloping) rather than those in a valley (Colorado, b). Behavior of *C. n. nelsoni* in El Dorado Co. Calif. is very similar; courtship sometimes occurs on flowers.

**Callophrys augustinus*. Males perch all day near the larval host in small open spots on ridges on the ground or larval host on the sunny side of the clearing, or on the uphill side of bushes where the ridgetop slopes downward from the crest (Douglas Co. Colo., b). In Nevada and Siskiyou and Alpine Cos. Calif. behavior is similar, males perch on top of shrubs on slopes or at the top of a slope, starting at 845 or earlier and continuing through the day (b). Powell's (1968) observations are similar although he did not observe perching in early morning probably due to unsuitable weather.

**C. polios*. Males perch all day in swales and narrow valley bottoms, in small clearings and on trails near the ground there, on or near the larval host (b).

**C. mossii*. Males in Jefferson & Boulder Cos. Colorado perch all day in gullies, in fairly open level sunny spots next to a sunlit bank of the gully (b). In San Mateo Co. Calif., males perch in a similar situation, on shrubs where a grassy hillside meets on a shrub belt extending to the valley bottom (c). In Nevada and Siskiyou Cos. California, males perch all day on top of shrubs sometimes at the upper part of a shrubless sloping swale or on prominent shrubs on a slope below an open space, but more often perch on shrubs at the top edge of a precipice (b).

**C. eryphon*. Males perch all day on the side of small trees (usually *Pinus ponderosa* in Colorado), about 2 m above the ground, almost exclusively in narrow valley bottoms and gulch bottoms (Jefferson County Colorado, b; El Dorado, and Siski-

you Cos. Calif., c).

**Callophrys apama*. Males perch all day in gullies on grass stems and other objects there (a).

C. dumetorum (Napa and Marin Cos. Calif., b) and *C. dumetorum viridis* (San Mateo Co. Calif., b). Males perch (and occasionally patrol) all day on small shrubs or other objects near the larval host, frequently on small or large hilltops.

C. affinis. Males perch all day on small shrubs (mainly *Artemisia tridentata*) on ridgetops and hilltops (Pitkin Co. Colorado; Lander Co. Nevada; Sweet Grass Co. Montana; c).

C. sheridani. Males perch all day near the larval host, in depressions on grassy hillsides, or occasionally in shallow roadside depressions, in Colorado (b) and southern New Mexico (c). In El Dorado and Alpine Cos. California (*C. s. lemberti*), males perch all day near the larval host in sheltered hollows, on shrubs or rocks or the ground (b). In Churchill Co. Nevada, *C. s. lemberti-comstocki* perched on shrubs or the ground in a gulch bottom next to a SW-facing slope (c).

Erora laeta quaderna. Males perch on top of trees on hilltops, at least in afternoon when observations were made (New Mexico, Arizona; c).

Phaeostrymon alcestitis. Males patrol about the canopy of *Sapindus drummondi* trees, the larval host, and often patrol during cloudy, windy, or rainy weather (as does *Hypaurotis crysalus* which has an almost identical mate-locating system.) Patrolling occurs from about 1400 to about 1800. In the morning males are mostly at flowers and mostly only females are found on the larval host trees; during the mating period both sexes occur on larval host trees (Baca Co. Colorado, b).

Habrodais grunus. Behavior is very similar to *H. crysalus*. Males start to patrol about *Quercus chrysolepsis* about 1400 and then patrol near the leaves until dusk. They patrol most frequently on the shady side of a group of trees. (Mt. Diablo, Contra Costa Co. Calif., c).

**Lycaena arota*. Males perch on branches of shrubs and trees 1-2 m above ground in small clearings in many different topographic situations, usually valley bottoms. A clearing likely to have a perching male is about 3-5 m in diameter, reasonably level, and surrounded by tall trees or steep hillsides. When abundant, males may perch at the side of large gulches where a few trees approximate a clearing. Males perch from about 0700 to as late as 1230. In El Paso County, Colorado, males

mostly stopped perching by about 1130, but in Chaffee County males stopped by about 1230 (part of this difference may be due to the sun rising earlier in El Paso than in Chaffee County) (a; Scott, 1974b).

**L. cupreus*. Males perch and often patrol all day in hollows of rockslides near the larval host (Clear Creek & Custer Cos. Colorado, c). In El Dorado Co. Calif., males patrol and sometimes perch all day mostly in rocky depressions (c).

**L. heteronea*. Males patrol all day, like the Plebejini they resemble, near the larval host (*Eriogonum umbellatum* in the Colorado Front Range) on hillsides etc. regardless of topography (b).

**L. xanthoides*. Males perch and occasionally patrol, all day on 1 m or less vegetation beside trails through fields or beside streams, and often court on flowers in afternoon (b, Jefferson Co. Colorado and Contra Costa Co. Calif.; Scott & Opler, 1975).

L. editha. Males perch all day in shallow narrow gullies and in shallow depressions in meadows, usually on low vegetation (Moffat Co. Colorado, and California, c).

**L. rubidus*. Males perch all day on vegetation in dry gullies and along streams, or along dirt trails through fields when high density fills more suitable sites (Colorado, b). The same behavior occurs in afternoon in Mono Co. California (c).

**L. thoe*. Males perch all day on vegetation 1 m or less above ground along streams and on prominent vegetation in or bordering a meadow where the larval host is abundant (b).

**L. helloides*. Males perch and sometimes patrol all day in depressions of wet meadows and especially along streams, usually on $\frac{1}{2}$ m tall vegetation. Males sometimes patrol especially in the montane meadows of Colorado, and mate-locating behavior occurs in wetter habitats than in *L. rubidus* (b). In Lander Co. Nevada males patrol and perch around *Polygonum* plants at least in afternoon (c).

L. nivalis. Males perch all day in shallow usually bare depressions, such as a shallow ($\frac{1}{2}$ m deep, 2 m broad) gully, and shallow depressions in an abandoned slightly inclined dirt road usually next to the valley bottom; the perching sites are hard to describe verbally, but males remain there often for most of a day (Gilpin Co. Colorado; Mono, El Dorado, and Siskiyou Cos. California; b).

L. gorgon. Males patrol and perch, all day on low vegetation near the larval hosts (California) (c).

L. mariposa. Males perch in hollows and valley bottoms in clearings often in dense forest, at least during midday (Yakima Co. Washington, c) and afternoon (Siskiyou Co. California, c).

**Hemiargus isola*. Males patrol erratically all day regardless of topography, often on flat land and in meadows where a larval host (*Trifolium repens*) occurs (c).

Hemiargus ceraunus. Males patrol erratically all day throughout the habitat, usually in valleys and on flats (Arizona, Mexico, c).

Leptotes marina. Males patrol very erratically (with a non-linear flight) all day throughout the habitat, usually in valley bottoms where most of the larval foodplants occur (c).

**Plebejus melissa*. Males patrol all day throughout the habitat, mainly near the larval hosts (b).

P. argyrognomon. Males patrol all day near the larval hosts on hillsides, flats, mainly in bunch-grassland near forest in Hinsdale Co. Colorado (c) or in moist meadows (Siskiyou Co. Calif., c).

**P. saepiolus*. Males patrol all day near *Trifolium*, the larval hosts, mainly in meadows, moist swales, and streamsides where these plants grow (b).

**P. icarioides*. Males patrol all day near *Lupinus* species, the larval hosts (b).

**P. acmon*. Males patrol all day near the larval hosts, wherever they grow on hillsides and flats, etc. (Colorado, California; b).

P. lupini. Males patrol all day about the larval foodplant *Eriogonum* plants (El Dorado Co., Nevada Co., Tulare Co. California; b).

**P. shasta*. Males patrol all day about 10 cm or less above the ground near the larval host in alpine cushion plant communities which have about 50% bare ground. These communities often occur on ridges and saddles and steep slopes (Colorado, b; Mono & Tuolumne Cos. Calif., c).

**Agriades glandon*. Males patrol all day near the larval hosts (*Androsace* species) often in valley bottoms.

**Brephidium exilis*. Males patrol all day around the larval hosts, which mainly grow on flats. Males fly weakly among and a few cm from branches of the larval hosts (Stockton, California; c).

**Glaucopsyche lygdamus*. Males patrol all day near the larval hosts in valley bottoms, hillsides, etc. (b).

**G. piasus*. Males patrol all day near the larval host (*Lupinus argenteus*) in valley bottoms or hillsides (b).

Philotes enoptes, **P. battoides*, **P. rita*. Males patrol all day on and between the larval host plants regardless of topography. Males and females often alight and feed on these plants (b for each species).

P. spaldingi. Males patrol all day near but not on *Eriogonum racemosum* (the larval host), patrolling more swiftly and erratically and slightly higher off the ground than the preceding three *Philotes* species. Males patrol in open pinyon-juniper woodland on flats and hillsides (b).

P. sonorensis. Males patrol weakly all day along the base of cliffs or sometimes on steep rocky slopes, always near the larval foodplants (California) (c).

P. speciosa. Males patrol all day about 6" above ground in swales or gully bottoms near the larval foodplant (Kern Co. Calif., c).

**Everes comyntas*. Males patrol all day near the ground near the larval host (*Trifolium repens* in Colorado), mainly in meadows and streamsides where this plant grows (b).

**E. amyntula*. Of all the Plebejini, this species most nearly approaches a perching species. Males often patrol, but often perch in depressions such as between a hillside and riparian shrubs or at the mouth of a tiny gully. Perching males investigate passing individuals, then patrol back and forth before returning to the vicinity of the previous perch. Mate-locating behavior occurs all day (Jefferson Co. Colorado; Siskiyou Co. Calif.; b).

**Celastrina argiolus*. In Napa Co. California males patrol all day over *Aesculus* trees throughout the habitat (c). Males patrol all day about shrubs and low trees, especially in valley bottoms and seldom on ridges etc. in Colorado (b). In southern Arizona and western Texas males often patrol about shrubs on hilltops (c).

HESPERIIDAE

**Epargyreus clarus*. Males perch in gullies on vegetation 1-2 m above ground. Perching starts about 0730 depending on temperature, and ends about 1315; after this period males mainly hang upside down from vegetation (b).

Zestusa dorus. Males perch on tips of branches of oak trees at the edge of a hilltop, at least in afternoon. Males also sit on

tree limbs overhanging streams where they feed on mud, but I have not yet seen perching behavior there; further observations are needed (southern Arizona, c).

**Thorybes pylades*. Males perch all day (few observations were made in afternoon) in gullies in west Texas and Colorado (c). In Utah and Arizona (Coconino Co.) and California (Colusa Co.) males perched all day on hilltops (c).

T. diversus. Males perch in tiny (often 3 m in diameter) forest openings where the presumed legume larval host is common on flat land and gentle slopes, at least 1330 to 1600 when observations were made (Tuolumne Co. Calif., b).

**T. mexicana*. Males perch all day on stones etc. on hilltops (Colorado, b; Tuolumne Co. California, c). *T. confusus* in central Texas perches on hilltops at least in afternoon (c) so may have similar behavior.

**Erynnis icelus*. Males perch and occasionally patrol, all day in slight depressions and shallow gullies near aspen trees (Gilpin Co. Colorado, b; Siskiyou Co. California, c).

**E. brizo*. Males perch all day on hilltops, often perching on the ground, sometimes on small shrubs. Males may fly back and forth before returning to a perch, which is a peculiarity occasionally seen in other *Erynnis* species also (b).

**E. persius*. Males perch all day on hilltops, on the ground and on low twigs often beside larger shrubs on the hilltop (a).

**E. afranius*. Males perch all day in gullies and swales, such as sunlit indentations in gully banks in morning and late afternoon, small gullies and narrow valley bottoms at midday (b).

**E. martialis*. Males perch all day on hilltops, mainly on the ground or on low twigs (b).

**E. telemachus*. Males perch all day in gullies, mainly on vegetation about 1 m above ground there (Colorado, a). In Colorado one copulating pair was found near a hilltop, and in Utah one male was observed perching on a hilltop.

**E. horatius*. Males perch all day on hilltops, usually on 1/3 m twigs, seldom on the ground (Colorado, b). In Texas males flew about small areas of hilltops before resting again, whereas Colorado males usually settled more rapidly.

**E. pacuvius*. Males perch all day on hilltops on low shrubs and other objects (in Jefferson and Douglas Co. Colorado, b; Colusa Co., California, c).

E. tristis. Males perch on hilltops all day, on barb-wire fence or a twig about 1 m above ground there. Males some-

times patrol about a few times before resting again (Napa Co. California, c).

E. propertius. Males perch all day, mainly in clearings on the sunlit side of ridgetops a few m from the ridgetop, but sometimes also on banks (such as roadcuts) in valley bottoms (California, b). *E. p. meridianus* males perch on hilltops all day (Coconino Co. Arizona and western Texas; c).

Autochthon cellus. Males perch in gullies on about 2 m tall vegetation, at least in afternoon when observations were made (Cochise Co. Arizona and western Texas; c).

**Pyrgus communis*. Males perch, and often patrol, all day, in swales and valley bottoms and similar situations. Perching males often patrol about a small area before returning to a perch. Males perch more when suitable depressions are available (b).

P. philetas. Males patrol and occasionally perch, in gulches and valley bottoms, waterholes, etc., all day (southern Arizona; c).

P. scriptura. Males patrol, and occasionally perch, all day in low areas of prairie, shallow gullies, and other depressions. Flight is only about 10-20 cm above ground (b).

**P. xanthus*. Males patrol, and often perch especially in gullies, all day near the larval host at high density, but at the usual low density males occur in small mostly dry gullies several meters deep and broad, where they often sit on the bottom or the sunlit side of the gulch (Colorado, New Mexico; b).

P. ruralis. Males patrol (and occasionally perch) about 10 cm above the ground all day, mainly in valley bottoms or grassy swales (Siskiyou and El Dorado Cos. California, c).

**P. centaurae*. Males patrol and occasionally perch, all day, in swales, valley bottoms, low spots next to bogs. Males perch more often at low temperatures, and patrol more often at high temperatures (c).

Staphylus ceos. Males patrol all day in gulches and valley bottoms, flying faster than *P. catullus* (southern Arizona, western Texas; c).

**Pholisora catullus*. Males patrol all day just above the ground in roadside ditches, gulches, dry reservoir bottoms, and other depressions (b).

**P. mejicanus*. Males patrol all day in the same manner and locations as *P. catullus*; the two species cannot be distinguished during flight (c).

**P. alpheus*. Males patrol in gullies and around the larval host shrubs, apparently all day (few observations were made in afternoon; c).

P. graciellae. Males patrol in gulches but mainly patrol through and around the larval host shrubs on flats, at least in morning and early afternoon (California, c).

P. libya. Males patrol in gullies and in and about the larval host shrubs at least in morning and early afternoon (Indio, California; c).

Systasea evansi. Males perch (they usually fly back and forth before resting again) in gulches apparently all day (few observations were made in afternoon) (southern Arizona, western Texas; c). *S. pulverulenta* had very similar behavior when observed at midday (western Texas; c).

Celotes nessus. Males patrol all day just above the ground (flight is rather weak) in gulches and along roadsides and other depressions. Males rest often so they may perch occasionally (southern Arizona, western Texas; c). *C. limpia* in western Texas with a longer distal prong on the male valva has nearly identical behavior (few observations; c).

Carterocephalus palaemon. Males perch on grass stalks and other objects about 1/3 m above ground, and often patrol as well, all day, in sedge swales in wet valley bottoms (Siskiyou Co. Calif.; c).

Copaodes aurantiaca. Males perch all day in gullies on vegetation about 1 m tall and have a very fast flight (Coconino Co. Arizona, southern Arizona and western Texas; b).

**Piruna pirus*. Males patrol all day usually in valley bottoms and gulches; males patrol several cm from the canopy of low plants averaging 1 m or less above ground, and patrol following the contours of the vegetation (b).

Ancyloxypha arene. Males patrol weakly all day over grass at the edges of springs and reservoirs (western Texas, southern Arizona; b).

A. numitor. Males patrol weakly all day over and among grasses at the edges of streams and reservoirs and at springs (Ohio, c; Yuma Co. Colorado, c).

Adopaeoides prittwittzi. Males patrol fairly weakly over watercress flowers and occasionally over grasses at a spring, at least in morning when observations were made (southern Arizona, c).

**Oarisma garita*. Males patrol weakly to rapidly all day in

tall grass of meadows, valley bottoms, and to a lesser extent on hillsides (b).

**O. edwardsii*. Males patrol often rapidly all day in grassy openings between shrubs, throughout the habitat but more often in valley bottoms than on hillsides (c).

**Yvretta rhesus*. Males perch all day on small (2 m tall) prairie mesa tops when these are present, on flat land occasionally (c).

Y. carus. Males perched at least from 1200 to 1400 when observations were made, on flat bare ground next to the probable larval host, a short grass growing next to a waterhole, and on sand bars. Females were mostly on the short grass, and some individuals fed on mud (Pima Co. Arizona; c).

**Stinga morrisoni*. Males perch all day on hilltops and ridges, often just below a shrub or between trees on the hilltop whereas *Hesperia pahaska* males usually perch in more open sites (b).

**Hesperia uncas*. Males perch all day on small (2 m tall) prairie mesa tops or small hilltops, but perch on smaller hilltops than most other *Hesperia*. *H. uncas* is very similar to *Y. rhesus* in behavior and appearance (b).

H. lindseyi. Males usually patrol slowly (about $\frac{1}{2}$ m per sec.) by fluttering about 15 cm above the grass, and males perch between these flights, all day, in grassland usually near the top of a ridge (Napa Co. Calif.; b).

**H. comma*. Males perch all day in southern Colorado and central Colorado (b) on hilltops. At high density at some localities (Chaffee and Jefferson Cos. Colorado, c) males investigate passing individuals while at mud. In Utah and Nevada and Mono Co. California, males of *H. c. harpalus* perch on hilltops or on flat areas when hilltops are not present, and males court at flowers (b). In El Dorado Co. California (c) males perched all day on the outer edge of a road on a steep slope. In Marin Co. California (c), *H. c. dodgei* males perched in bunch grass where the local population occurs and not on adjacent hilltops where *H. columbia* perches.

H. juba. Males perch all day in gullies, rocky depressions, and valley bottoms, both in Jefferson Co. Colorado (c) and in El Dorado Co. California (c).

**H. nevada*. Males perch all day on small to large hilltops and ridges (Custer and Park Counties Colorado, b; Tuolumne Co. California, c).

**H. viridis*. Males perch all day on rocks or bare ground of gullies and valley bottoms (Colorado, b; Texas, c).

H. columbia. Males perch all day on ridgetops and hilltops on low shrubs and rocks (Marin and Napa Counties, California, b).

**H. pahaska*. Males perch all day on hilltops and ridgetops on rocks or short plants (a; Scott, 1973d).

**H. leonardus pawnee* and *H. l. montana*. Males perch all day on small to large hilltops, or on flats near *Liatris punctata* flowers (b).

H. ottoe. Males perch all day on flowers, especially thistle. Males almost never occur away from these flowers, and by releasing other individuals near males on flowers it was found that males investigate other individuals all day. These flowers occurred in a valley bottom (Boulder Co. Colorado, c).

H. miriamae. Males perch all day on rocks or sometimes on the ground (especially those rocks that are sunlit and out of the wind) on alpine hilltops and ridgetops. Males have an extremely fast flight (Inyo and Mono Co. California, c).

H. woodgatei. Males perch all day on hilltops where they sit on rocks etc. on or near the ground (southern Arizona, c).

Hylephila phyleus. Males perch all day on prominent plants or hedges on lawns, grassy swales, and similar sites (Clark Co. Nevada, c; Yolo Co., California, c).

**Atalopedes campestris*. Males perch all day in grassy meadows and swales Fremont Co. Colorado, c; central Texas, c).

Nastra julia. Males perch all day in grassy swales such as along roads and irrigation ditches (SW of Parker, Arizona; c).

Lerodea eufala. Males perch all day in grassy swales and flats, along irrigation ditches (SW of Parker, Arizona, c; Yolo Co. California, c).

L. arabus. Males perch all day in gulches and along streams near large clumps of the presumed larval host grass. Males perch on vegetation as much as a meter above ground (Pima Co. Arizona, c).

Paratrytone melane. Males perch all day in grassy swales, gullies, lawns (California, c).

**Polites origenes*. Males perch all day in grassy swales and openings in valley bottoms (b).

**P. themistocles*. Males perch all day in grassy swales, depressions in meadows and lawns (b).

P. mystic. Males perch all day in low spots of meadows and

grassy streambanks (b).

**P. sonora*. Males perch all day in low spots of moist grassy meadows (Park, Chaffee, and Saguache Counties Colorado, c). In El Dorado and Tulare Counties California, behavior was similar but at high density courtships were frequent at flowers (c).

**P. sabuleti*. Males perch all day in low spots of alkaline flats where larval host is abundant, in low spots of meadows, and on flowers on flat land (Colorado, Clark & Nye Cos. Nevada, Mono & Inyo Cos. California, Emery & Millard Cos. Utah; a).

**P. draco*. Males perch all day in low spots of meadows and in gullies (b).

P. coras. Males perch all day in grassy swales and low spots of meadows (c).

Ochloides sylvanoides. Males perch all day in gullies and valley bottoms on vegetation about 1 m above ground (Colorado, b). In Yolo Co. California, males perch in nooks among shrubs, often on ridgetops (c).

O. agricola. Males perch mainly in the shade of shrubs about 1/3 m above ground at the edges of clearings throughout the habitat, and males often court at flowers all day.

O. yuma. Males perch all day in low spots near the larval host, especially in depressions between this host (*Phragmites*) growing at a river edge and the bank. Males perch on large rocks or 1 m tall vegetation (California, c; Mesa Co. California, b).

**O. snowi*. Males perch all day in gullies on rocks or 1 m vegetation, and some courtships occur at flowers (a; Scott, 1973d).

**Poanes taxiles*. Males perch all day in gullies and valley bottoms, especially in shaded areas, on vegetation about a meter or more high. Males perch in more shaded locations and in cloudier weather than does *Poanes hobomok* (a).

**P. hobomok*. Males perch all day on vegetation about 2 m above the bottom of gullies and valley bottoms (b).

**Atrytone delaware*. Males perch all day in grassy swales, mainly in valley bottoms (b).

A. arogos. The main activity of both sexes is feeding on flowers. However, feeding males do not investigate individuals released nearby (contrasting with *H. ottoe*). After many failures in observing interactions at flowers I finally observed males perching on low (about 10 cm) vegetation on a gently sloping base of a hillside covered with *Andropogon*, the larval host.

A few males perched in a grassy swale below a similar slope. In three days observations perching started about 1320 and continued until late afternoon until rain or clouds stopped activity. This mating period is strange because it occurred during cloudy and sometimes rainy weather; perching males were often seen to rapidly vibrate their wings during cloudy periods, apparently as a heat gain device (shown to raise body temperature by Krogh & Zeuthen, 1941; Kammer, 1970). Additional observations are desirable to confirm this mating period (c).

**Euphyes vestris*. Males perch in gullies all day on about 1 m vegetation (Colorado, a; in California males perch in swales in coastal meadows, c).

E. bimacula. Males perch all day in low spots of moist sedge marshes, on about 1 m stalks of clumps slightly taller than surrounding vegetation (Yuma Co. Colorado, c).

**Atrytonopsis hianna*. Males perch all day on or near the ground on 2-4 m wide relatively flat clearings of valley bottoms, and occasionally in similar situations on slopes near the larval host (c).

**A. vierecki*. Males perch all day in gulches, usually on 1 m tall vegetation (Colorado, c; Cimarron Co. Oklahoma, c).

A. cestus and *A. ovinia*. In two days observations in Pima Co. Arizona, males perched on rocks on south-facing sides of gullies, especially gullies 3-7 m high next to hillsides and flowers. Males perched from early morning to about 1200, and in afternoon fed on flowers and rested (without interacting) on gully walls (c for each).

A. pittacus. Males perch all day, almost always in gullies in southern Arizona and western Texas (c), although near Alpine, Texas males also perched in a depression on the sloping leeward side of a hilltop about 3 m from the top (c).

**Amblyscirtes simius*. Males perch on top of small prairie plateaus, ridgetops and hilltops, from about 0740 to about 1050, with maximum perching from 0830 to 0930 (a; Scott, 1973c).

**A. aenus*. Males perch all day in gully bottoms, especially on rocks in rocky areas of the gully (b).

**A. vialis*. Males perch all day in narrow valley bottoms with much vegetation, usually perching on 1 m vegetation (b).

**A. oslari*. Males perch all day in gully bottoms and roadside ditches, especially in sandy spots on the gully bottom (b).

**A. eos*. Males perch all day in gullies and valley bottoms, on flat usually grassy spots on or just beside the gully bottom (c).

**A. phylace*. Males perch all day in mostly bare depressions, such as a depression at the mouth of a small gully opening onto a flat, a roadside cut below a small gully, etc. The perching locations change throughout the day as males choose sunlit locations (b).

A. nysa. Males perch all day near or on the bottom of narrow gullies (Texas, c).

A. texanae. Males perch all day in gullies on rocks or other objects (western Texas, c).

Agathymus mariae. Males perch in morning near the larval host (western Texas, c).

A. remingtoni estelleae. Males perch in morning near the larval host, especially at the base of a slope (western Texas, c).

**Megathymus streckeri*. Males perch on hillsides and flats near the larval host. My observations were only in morning, but Scott Ellis (written communication) has observed mating at 1300 in *M. s. leussleri* and much chasing between males in late afternoon in *M. s. streckeri* in southern Colorado (c). Mr. Kilian Roever, however, states (pers. comm.) that male activity in *M. s. streckeri* and *M. yuccae* ceases after midday.

**M. yuccae*. Males perch near the larval host at least in morning (c). Scott Ellis (pers. comm.) has observed strong perching behavior from about 0900-1100, "but the males seem to disappear in the afternoon."

DISCUSSION

Before making generalizations, I will mention some of the most unusual species. Some species both perch and patrol frequently (most perching species patrol infrequently, and many patrolling species sometimes perch). The best examples are most *Oeneis* and *Pyrgus* species; others are the *Papilio machaon* group (*P. zelicaon*, *bairdii*, *polyxenes*), *P. eurymedon*, *Limenitis wiedemeyeri*, *Nymphalis antiopa*, *N. californica*, *Phyciodes mylitta*, *P. pallida*, *P. texana*, *Euphydryas* spp., *Poladryas minuta*, *Chlosyne palla*, *C. acastus*, *C. gorgone*, *C. lacinia*, *C. leanira*, *C. theona*, *Calephelis nemesi*, *Lycaena cupreus*, and *Everes amyntula*. *P. minuta* differs from the others in that males mainly perch in the morning, but mainly patrol in the afternoon. *Speyeria callippe* is unusual in that the location of patrolling changes somewhat during the day. In several patrolling species, males seem to patrol about the tops of shrubs late in the day, apparently seeking roosting females (*Boloria titania*, *Plebejus melissa*).

The study of mate-locating behavior provides numerous useful taxonomic characters. For instance, in *Amblyscirtes* the three species groups previously recognized on morphological grounds also differ in mate-locating behavior. *A. simius* differs from other *Amblyscirtes* by mating only part of the day and on ridgetops but not in gullies; *A. phylace* differs by mating at the mouth of small gulches and in roadside ditches (the other *Amblyscirtes* mate in deep gullies). Perching or patrolling behavior and the time of day of mating seem to be rather conservative characters that are useful in comparing genera or higher taxa; the location of mating often differs between congeneric species and is very useful for intrageneric classification.

Location of mating can be placed into two general categories: 1) mating primarily occurs near the larval foodplants; 2) alternatively, mating occurs in specific topographic sites regardless of the distribution of the larval foodplants. If the larval foodplants are generally distributed within the flight area of the population regardless of topography (such as throughout a bog in a bog species, or throughout the habitat) patrolling behavior seems to be the usual mate-locating method, but often mating occurs in specific topographic sites such as gullies or hilltops (such as some *Hesperia* species that feed as larvae on widespread grasses). If larval foodplants are spotty in distribution within the normal flight area of a population (such as *Apodemia nais* which feeds on *Ceanothus fendleri*) perching behavior seems to be the usual strategy. If the foodplants are linearly distributed (such as streamside willows), in many species males patrol along the stream (*Limenitis achippus*), and in some species males perch there (*Satyrrium sylvinus*).

The strategy of mating in topographically distinct sites is often used for bringing the sexes together in species in which the larval foodplants occur throughout the habitat. Often several types of sites appear adequate to this function: closely related species may mate in different types of sites.

I found that eighteen congeneric pairs of butterflies rendezvous for mating in contrasting topographic sites. These eighteen pairs are listed below. The first species of the pair mates on hilltops, the second species in gulches, valley bottoms, or, for *P. indra*, rocky outcrops just below a hilltop. The foodplants of the species as larvae are listed. Localities studied are listed. 1) *Papilio eurymedon* (*Ceanothus fendleri*; Red Rocks, Jefferson Co. Colorado) and *P. multicaudata* (*Prunus virginiana*;

Red Rocks, and Jarre Canyon, Douglas Co. Colorado, Hardscrabble Canyon, Custer Co. Colorado). 2) *P. zelicaon* (*Harbouria trachypleura*; Red Rocks) and *P. indra* (*H. trachypleura*; Red Rocks). 3) *Euchloe olympia* (various Cruciferae undetermined for Colorado; Red Rocks, Jarre Canyon, and the Arkansas River Canyon, Fremont Co. Colorado and NW of Pueblo, Colorado) and *E. ausonides* (various Cruciferae; Red Rocks, Jarre Canyon, Hardscrabble Canyon). 4) *Pieris sisymbri* (various Cruciferae undetermined for Colorado; Jarre Canyon, Arkansas River Canyon, and NW of Pueblo) and *P. chlorodice* (= *beckeri*) (Arkansas River Canyon, NW Pueblo; various Cruciferae such as *Stanleya pinnata*). 5) *Oeneis melissa* (unknown monocotyledons; Loveland Pass and Mt. Evans, Clear Creek Co. Colorado) and *O. polixenes* (same foodplants and localities). 6) *O. chryxus* (unknown grasses; Jarre Canyon, and Gregory Canyon, Boulder Co. Colorado, and Greenhorn Peak, Huerfano Co. Colorado, and Rosita, Custer Co. Colorado) and *O. uhleri* (unknown grasses; same localities except for Rosita). 7) *Speyeria callippe* (*Viola*; Red Rocks) and *S. atlantis* (same foodplants and locality, Arkansas River Canyon). 8) *Chlosyne gorgone* (*Helianthus pumilus*; Red Rocks, Hardscrabble Canyon, and Green Mountain, Jefferson Co. Colorado) and *C. nycteis* (*Rudbeckia laciniata*; same localities except for Green Mountain). 9) *Nymphalis californica* (*Ceanothus fendleri*; Jarre Canyon) and *N. antiopa* (*Salix*, *Populus*, *Ulmus*, *Celtis*; Red Rocks, Jarre Canyon, Gregory Canyon, Hardscrabble Canyon). 10) *Callophrys augustinus* (*Arctostaphylos uva-ursi*; Russel Ridge, Douglas Co. Colorado) and *C. polios* (*A. uva-ursi*; Gregory Canyon, Russel Ridge). 11) *Satyrium californica* (*Ceanothus fendleri*; Red Rocks) and *S. acadica* (*Salix exigua*; Canon City, Fremont Co. Colorado). 12) *Thorybes mexicana* (various Leguminosae undetermined for Colorado; Red Rocks, Greenhorn Peak) and *T. pylades* (same foodplants; Red Rocks). 13) *Erynnis brizo* (*Quercus gambellii*; Red Rocks, Jarre Canyon) and *E. icelus* (*Populus tremuloides*; Central City, Gilpin Co. Colorado). 14) *Erynnis persius* (*Astragalus*, *Thermopsis*, and other legumes; Red Rocks, Jarre Canyon, Rosita, Arkansas River Canyon) and *E. afranius* (*Astragalus*, *Lupinus*, *Lotus*, and other legumes; Red Rocks, Green Mountain, and Wetmore, Custer Co. Colorado). 15) *Erynnis horatius* (*Quercus gambellii*; Red Rocks, Jarre Canyon, Oak Creek Canyon S. of Canon City, Colorado) and *E. telemachus* (same foodplant; same localities

and Hardscrabble Canyon). 16) *Hesperia pahaska* (*Bouteloua gracilis*; Red Rocks, Green Mountain, Arkansas River Canyon, Platte River Canyon, Douglas Co. Colorado) and *H. viridis* (*B. gracilis*; same localities except Platte River Canyon, and Pueblo, Colorado, and Black Mesa, Kenton Co. Oklahoma). 17) *Hesperia comma* (various grasses; Red Rocks, Arkansas River Canyon, Rosita, Platte River Canyon) and *H. juba* (various grasses undetermined in Colorado; Red Rocks, Green Mountain). 18) *Amblyscirtes simius* (*B. gracilis*; Arkansas River Canyon, and near Saguache, Saguache Co. Colorado) and *A. oslari* (grasses undetermined in Colorado; Red Rocks, Arkansas River Canyon, Gregory Canyon, Hardscrabble Canyon).

The use of separate mating sites by these congeneric species certainly prevents, and may result from, interference competition during mate-locating behavior. Interference between butterflies during mate-locating behavior arises from the generalized nature of the stimuli involved in visual communication between the sexes (Scott, 1973a, 1974a). Mate-locating behavior is a process of screening flying or resting objects for receptive females. Perception of the insect compound eye is poor for shapes, but good for movement. The size and color pattern of the two species of a pair is very similar in most cases. Males probably cannot distinguish color pattern differences as small as those between most of the congeners. Male butterflies sometimes investigate resting individuals, and often investigate aerial objects of a great variety of shapes and colors including other insects, birds, etc. Pheromones which might enable interspecific males to avoid interaction are currently unknown. Both perching and patrolling species appear to delineate a space around them in which moving and occasionally resting objects are investigated ("moveable individual space"). Two congeneric males do not occur in the same space for long because investigative interactions occur after which at most one male remains. Intense con- and interspecific interactions occur where males are concentrated. These interactions result in interference competition for time, space, and energy; time is lost (in which a passing female might be missed), the probability of being in a favorable mating arena is less, energy is wasted, and courtships with receptive females are often disrupted (another male often investigates a courting pair and the two males then often interact, ending courtship).

In some of these congeneric pairs interference competition

itself may have resulted in the evolution of separate mating sites. If two species have the same mating sites and if interference competition between them is great, when a mutation for mating at another site arises in one species (especially the rarer species) mating may be more successful at the second site and the proportion of individuals of that species mating there will gradually increase, ultimately resulting in genetic fixation. As selection proceeds, as the proportion of the selected species mating at the first site drops the selection against those mating at the first site will intensify because an increasing proportion of individuals encountered there will be nonconspecific. Rapid fixation of mating at the second site for the one species will then occur due to the continual increase of selection intensity against mating at the first site. This mechanism would be most rapid in two species which are postzygotically, but not prezygotically, reproductively isolated, which could occur if postzygotic but not prezygotic reproductive isolation developed in two allopatric populations which then became sympatric.

Most butterfly species mate at any time of day. Restricted time of day of mating occurs often in some taxa (Nymphalini, Riodininae, Theclini, Megathyminae), rarely in other taxa (Satyrinae, Apaturini, Lycaenini, Pyrginae, Hesperinae), and with my current knowledge not at all in many taxa (Papilionidae, Pieridae, Argynnini, Melitaeini, Limenitini, Charaxinae, Danainae, Plebejini).

There is an altitudinal trend in the time of day of mating. Of 284 species for which mate-locating behavior is reported herein, only 35 mate during a restricted part of the day (included are five species, *Vanessa* spp. and *Asterocampa celtis*, which seem to mate more frequently late in the day). All of these 35 species are primarily desert, foothills, or plains species rather than high mountain species. The primarily high mountain species all mate at any time of day.

Inclement weather is frequent in spring and fall. It is significant that only two species that mate during only part of the day are univoltine and mate in the spring (*Megathymus yucca*, *Polygonia faunus*). In *P. faunus* long life of the hibernating adults allows them to wait for good weather. The other species are univoltine and emerge in summer, or are multivoltine.

Mate-locating is an energy-demanding process, and greatly exposes males to predation. Perhaps more dependable weather in the foothills and plains compared with the alpine zone, and

in summer compared with spring, allows some species to reduce the hours devoted to mating (and sometimes reduced adult feeding) without seriously decreasing the proportion of females mating. At high altitude and in early spring, however, inclement weather requires that animals make use of all available periods of suitable weather, no matter what time of day these occur. Time of day of mating seems to have evolved as a compromise between energy (and predation?) losses and inseminating the maximum number of females.

Those species which mate only in early morning or in afternoon and early evening mate on sunlit areas such as treetops and hilltops; species mating at other times can mate in gullies and other locations that do not receive early and late sunlight.

Scott and Scott (1976) present an ecological analysis of the butterflies of an area of southern Colorado. I determined mate-locating behavior of the species in that area, and the following analysis attempts to determine how the behavioral and ecological characteristics of a species influence or are influenced by its mate-locating behavior.

To quantify mate-locating behavior, the following three qualitative indices were constructed: a) perching-patrolling index (1-males almost always perch prior to encounters; 4-males almost always patrol prior to encounters; 2 and 3 intermediate); b) location of mating index (1-mate in quite restricted sites of the habitat such as hilltops; 4-mate almost anywhere in the habitat; 2 and 3 intermediate); c) time of day of mating index (duration of the daily mating period of a species in hours, divided by 2; a mating period of "all day" is assumed to be 8 hours in duration).

Perching species in southern Colorado have a strong tendency to mate in restricted sites in the habitat, as predicted by Scott (1974a). The evidence is that the correlation (product-moment) between the perching-patrolling index and the location of mating index for the 159 species is .54 ($p < .01$), which means that perching species tend to mate in restricted sites and patrolling species tend to mate more generally in the habitat.

Perching species in southern Colorado also tend to mate only during restricted times of day rather than at any time of the day. The correlation between the perching-patrolling index and the time of day of mating index is .34 ($p < .01$).

Perching behavior in southern Colorado is much more common in species that have only 1 or 2 broods during the season

than in species with 3-4 broods (Table 1).

No consistent changes of mate-locating behavior with altitude were observed for the southern Colorado butterflies, except that above timberline all the species mate all day, and almost all species patrol there.

Southern Colorado butterflies that emerge at the end of the season tend to have patrolling behavior and tend to mate throughout the habitat much more frequently than species that emerge at the start of the season (Table 2).

The 159 species were placed into five categories depending on the meagre (usually) to extensive data I have concerning their movements (Scott, 1976). The only trends found (Table 3) are that species with very large movements more often tend to be patrolling species and to mate throughout the habitat.

No consistent relationship between the frequency with which a southern Colorado species feeds on flowers of the larval host and mate-locating behavior was observed.

Larval foodplants of the southern Colorado butterflies were given by Scott and Scott (1976). Tables 4 and 5 relate mate-locating behavior to the larval foodplants. Species feeding on shrubs or trees rather than on herbs more often tend to be perching species and more often tend to mate during a restricted period during the day.

I now attempt to determine the effect of the distribution of larval foodplants on mate-locating behavior in a different way, by examining the mate-locating behavior of various western U. S. butterflies that have the same larval foodplants, to discover whether convergent evolution occurs. The following comparisons were made.

1) *Ceanothus fendleri* (plants spottily but sometimes generally distributed on south-facing hillsides and dry valley bottoms). Mating generally occurs in hilltops or gulches: *Erynnis pacuvius*, *E. martialis*, *Papilio eurymedon*, *Satyrrium saepium*, *S. californica*, and often *Nymphalis californica* mate on hilltops (*N. californica* sometimes mates in gulches etc.), and *Apodemia nais* mates in low spots in gulches near *Ceanothus*.

2) *Eriogonum umbellatum* (generally distributed on steep hillsides, mesas, and other locations). Two strategies occur. *Plebejus acmon*, *Philotes enoptes*, and *Lycaena heteronea* patrol regardless of topography (*L. heteronea* is the only *Lycaena* with mainly patrolling behavior, and has apparently convergently evolved patrolling behavior). *Callophrys sheridani*, *C. affinis*,

and *C. apama* (this species probably feeds on *E. umbellatum*, but no proof exists) mate in hilltops, gullies, or hillside depressions depending on the species.

3) *Salix exigua* (linearly clumped distribution along streams and irrigation ditches). Two strategies occur. *Satyrium sylvinus* and *S. acadica* perch on the plant, while *Nymphalis antiopa* and *Limenitis weidemeyeri* perch in valley bottoms near willows. *Papilio rutulus* and *L. archippus* patrol near the willows. The difference in strategy of the two *Limenitis* may be due to their different habitats: *L. archippus* occurs on the plains where *S. exigua* is more continuously distributed, whereas *L. weidemeyeri* occurs mainly in the foothills (and larvae feed on other Salicaceae as well) where the foodplants are more spotty and there are more varied topographic sites.

4) *Quercus gambellii* (generally distributed, sometimes in groves). In *Hypaurotis crysalus*, in which all activities are carried out on the plant (Scott, 1974), males patrol. *Satyrium calanus*, *S. liparops* (which may not feed on this oak species in Colorado), *Erynnis telemachus*, *E. brizo*, and *E. horatius* mate in gulches or hilltops.

5) *Prunus virginiana* (usually in small groves, mainly in valley bottoms). *Papilio multicaudata* patrols up and down valley bottoms, but *Harkenclenus titus* perches on hilltops.

6) *Sedum lanceolatum* (generally distributed on hillsides, etc.). *Parnassius phoebus* patrols on hillsides and meadows near the plants, but *Callophrys mossii* perches in gullies and is a foothills species whereas *P. phoebus* usually occurs in grasslands at higher altitude.

7) *Pinus* species (generally distributed). *Neophasia menapia* patrols throughout the habitat, but *Callophrys eryphon* perches in gulch bottoms.

8) *Ribes* species (throughout the habitat, but more often in valley bottoms). *Polygonia zephyrus* and *Lycaena arota* both perch mainly in valley bottoms.

9) *Celtis reticulata* (in groves on flats and in valley bottoms). *Asterocampa celtis*, *Nymphalis antiopa*, and *Polygonia interrogationis* all perch in valley bottoms on or near the *Celtis* plants.

10) *Cirsium* spp. (clumped weeds often on disturbed areas). *Vanessa cardui* perches often on hilltops (and feeds on many

other plants as larvae), whereas *Phyciodes pallida*, *P. mylitta*, and *P. orseis* mainly perch in gullies.

11) *Sphaeralcea coccinea* (widely distributed, mainly on flats). *Vanessa caryae* perches often on hilltops, but *Pyrgus scriptura* and *P. communis* patrol and perch in swales.

12) *Atriplex* spp. (clumped in alkaline areas usually on flats). *Brephidium exilis*, and *Pholisora alpheus* and its congeners, patrol near *Atriplex*, or patrol in gullies (*Pholisora*).

13) *Astragalus* spp. (mostly generally distributed in open areas). Most species patrol (*Colias eurytheme*, *C. philodice*, *C. alexandra*, *Hemiargus isola*, *Leptotes marina*, *Everes amyntula*, *Plebejus acmon*), but *Erynnis persius* perches on ridgetops.

14) *Lupinus argenteus* (clumped, often in valley bottoms on deep soil). *Plebejus icarioides*, *Glaucopsyche lygdamus*, and *G. piasus* patrol, but *Erynnis afranius* perches in gullies.

15) *Trifolium* (usually clumped in moist meadows except near timberline). *Colias cesonia*, *C. meadii*, *Plebejus saepiolus*, and *Everes comyntas* patrol, but *Thorybes pylades*, which has other hosts, perches in gulches.

16) *Bouteloua gracilis* (very widely distributed). *Neominois ridingsii*, *Amblyscirtes simius*, *Yvretta rhesus*, *Hesperia pahaska*, *H. viridis*, *H. uncas*, and *H. comma* all mate on hilltops or gulches.

It is clear from the above mate-locating behavior of species with the same larval foodplants that for a given situation there is usually more than one strategy of locating females. Behavior is likely to be similar in taxonomically closely related species. Distantly related species often have different behavior, but sometimes they have convergently evolved the same behavior. Perhaps the most spectacular examples of convergence are *Philotes* and *Lycaena heteronea*, and *Neominois ridingsii* and *Amblyscirtes simius*.

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Table 1. Change of behavioral characteristics with number of broods. *Brephidium exilis*, with 5 broods, is placed with the 4-brood group. Figures are averages. Means and standard deviations for all the variables for all 159 species are also given.

No. of broods	Number of Broods				Mean	Standard Deviation
	1	2	3	4		
No. of species	108	22	17	12	159	159
Perching-patrolling Index	2.32	1.93	2.82	3.58	2.41	1.41
Location of Mating Index	2.28	1.87	2.29	2.83	2.27	.88
Time of Day of Mating Index	3.76	3.42	3.85	3.83	3.73	.67

Table 2. Change of behavioral characteristics throughout the season for single brood species only. Figures are averages.

	Time of Emergence							August-early Sept
	May	early June	mid June	late June	early July	mid July	late July	
No. of species	12	12	13	10	19	14	16	11
Perching-patrolling Index	1.83	1.92	1.85	1.60	2.74	2.14	2.87	3.18
Location of Mating Index	1.92	1.92	2.23	1.80	2.42	2.14	2.75	2.86
Time of Day of Mating Index	3.55	4.00	4.00	3.63	3.83	3.66	3.46	4.00

Table 3. Means of behavioral characteristics for species with different magnitude of movements.

	Magnitude of Movements				Migrate Thousands of Kilometers
	Very Local-ized Species	Neither Migratory or very Local	Apparently Can Move Several Kilometers	Can Move Several Kilometers	
No. of species	24	102	16	15	2
Perching-patrolling Index	2.29	2.20	2.62	3.80	2.50
Location of Mating Index	2.04	2.18	2.12	3.40	2.00
Time of Day of Mating Index	3.35	3.84	3.35	4.00	3.50

Table 4. Means of behavioral characteristics for species with different larval foodplants.

Larval Foodplants	No. of Species	Perching-Patrolling Index	Location of Mating Index	Time of Day of Mating Index
Salicaceae	10	2.40	2.10	3.30
<i>Prunus</i>	3	2.00	1.67	3.60
<i>Rumex</i>	5	1.40	1.80	4.00
<i>Asclepias-Croton-Celtis</i>	3	2.00	1.67	3.73
<i>Urtica</i>	4	1.00	2.00	2.35
Malvaceae	3	2.00	2.33	3.50
Chenopodiaceae-Amaranthaceae	4	4.00	2.00	4.00
<i>Ribes</i>	2	1.00	2.00	2.10
<i>Sedum</i>	2	2.50	3.00	4.00
<i>Androsace</i>	1	4.00	4.00	4.00
<i>Viola</i>	7	4.00	3.43	4.00
Ericaceae	3	2.00	2.00	4.00
<i>Potentilla</i>	2	2.50	2.00	4.00
Scrophulariaceae	3	2.50	2.67	4.00
Compositae	11	3.00	1.91	3.77
<i>Cercocarpus</i>	1	1.00	1.00	4.00
<i>Quercus</i>	5	1.60	1.80	3.56
<i>Pinus-Juniperus-Arceuthobium</i>	4	1.75	2.75	4.00
<i>Ceanothus</i>	4	1.25	1.25	2.87
<i>Eriogonum</i>	7	3.14	3.43	3.67
Leguminosae	18	3.11	2.83	3.94
Umbelliferae	2	3.00	2.00	4.00
Cruciferae	9	4.00	2.11	4.00
Polyphagous (<i>S. melinus</i> , <i>C. argiolus</i>)	2	2.50	2.00	3.00
Grasses or sedges	42	1.81	2.06	3.88
<i>Yucca</i>	2	1.00	3.00	2.65

Table 5. Means of behavioral characteristics for species feeding on herbs and on shrubs.

	Herbs	Shrubs-Trees
Perching-Patrolling Index	2.54	2.10
Location of Mating Index	2.29	2.20
Time of Day of Mating Index	3.84	3.46

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HISTORY OF SCIENTIFIC STUDY ON A LARVAL COLOR POLYMORPHISM IN THE GENUS *CHLOSYPNE* (NYMPHALIDAE)

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A STRIKING POLYMORPHISM involving larval color is manifested in two species of melitaeine butterflies, *Chlosyne lacinia* (Geyer) and *Chlosyne gorgone* (Hubner). Each species exhibits three morphs: 1) *rufa*, an orange form, 2) *nigra*, a black form and 3) *bicolor*, a black form with a row of orange spots along the mid-dorsal line giving the appearance of a broad stripe. The larval morphs of *C. lacinia* were illustrated in natural colors by Neck et al. (1971). The resemblance of the polymorphic larvae of these two species is remarkable. Genetic studies have revealed that the inheritance mechanisms are identical in both species (Neck et al., 1971; Neck, 1973b). The polymorphism is believed to be homologous in that it is probable that both species are derived from a common ancestor which was also polymorphic for larval color patterns (Neck, 1973b). Remarkably, there has been no scientific study of these polymorphisms until the past several years.

The difference between the comparable morphs of these two species are diagnostic but very minor. The *gorgone rufa* is a yellowish orange while the *lacinia rufa* is orange to orange-red. This is true as well for the stripe of the comparable bicolor morphs. The mid-dorsal spots of the *gorgone bicolor* are strictly square-like in configuration while the spots of the *lacinia bicolor* are more variable and less distinct in shape and tend toward ovoid in some individuals. The melanized portions of the bicolor morph and *nigra* morph of *gorgone* appear to be somewhat darker than the comparable portions of *lacinia* larvae. This results in a greater contrast between the dark background and the lighter stripe of the bicolor morph in *gorgone* than in *lacinia*.

Larval Descriptions By W. H. Edwards

Edwards (1893) reported the initial description of *lacinia* larvae (as *Synchlœ lacinia* Geyer) as quoted from a letter by T. D. A. Cockerell—"1. nigra, a black form. 2. bicolor, a black with broad dorsal stripe. 3. rufa, a red form." Edwards (1893) also described *lacinia* larvae in his own words as follows: "There are at least three distinct types of larva: 1st.—All red- or yellow-fulvous. 2nd.—The dorsum and lower part of side fulvous, the sub-dorsal areas dark brown. 3rd.—All black, or black with a greenish band on each side." Note the reversal of order of nigra and rufa.

The following year Edwards (1894) described samples of *gorgone* larvae (reported as *Phyciodes carlota* Reakirt) which he had reared simultaneously with the *lacinia* larvae. His description (from three larvae) fits the bicolor morph—"deep black . . . ; a red-fulvous mid-dorsal band" Although he received eggs from Colorado and larvae from Montana, most of his larvae entered diapause before maturing. His original samples may have contained individuals of one or both of the other morphs. The color polymorphism is quite muted in diapausing individuals.

It is surprising that Edwards did not refer to a resemblance of the bicolor larvae of these two species. Although he quoted from a letter by Cockerell in describing *lacinia* larvae, Edwards reared larvae of the two species concurrently. He further stated, "The eggs of the two are in no way distinguishable, nor are the larvae in the first two stages; as regards shape and armature they are alike in the succeeding stages, but differ in coloration." Edwards apparently did not consider the larvae to be similar due to the interspecific differences discussed above. Possibly, the larvae were affected by rearing conditions, long overland mail travel, or entered diapause, all of which are known to affect larval coloration.

Subsequent Descriptions of *lacinia* Larvae

Other less complete descriptions of the larvae of *lacinia* have appeared in the American scientific literature. Comstock (1927: 119) reported the larvae as being "so variable in color as to be described with difficulty. The range is from a solid black to a reddish-fulvous, with a variety of stripes and blotches." Later, Comstock (1946) reported the larvae of this species to be "extremely variable in pattern and color." Tinkham (1944)

merely referred to the "spiny caterpillars" of *lacinia*. Thorne (1962) mentioned that "the few orange caterpillars of *lacinia* were conspicuous among the dark *californica* larvae." It is quite likely that he overlooked the nigra *lacinia* larvae as they look much like the black larvae of *Chlosyne californica* (Wright) as described by Comstock (1929). Thorne makes no mention of bicolor-type larvae.

Descriptions of *lacinia* larvae originating from Latin American populations were also published. Koehler (1927) reported upon the biology of *lacinia* (as *Chlosyne saundersi* Dbl. & Hew.) from observations in northern Argentina at the southern edge of the geographical range of *lacinia*. He reported that the larvae vary from bright reddish brown to almost black. The dark form contained many spots, dorsal, lateral or both (an apparent reference to the bicolor morph). ("Su color varia de marron rojizo claro al casi negro. En la forma oscura observamos muchas veces manchas dorsales o laterales o ambas. . .") Dyar (1911) gives a perfect description of a rufa larva as follows: "Body red-brown, marked transversely with black lines, two on each segment behind the spines. . . ." This description was made from an inflated specimen originating from an undefined locality in Mexico. It is pertinent here to mention that *lacinia* is not listed in monographs on the nymphalid larvae of South America (Muller, 1886) or life histories of Mexican lepidoptera (Comstock and Vasquez, 1961).

Subsequent Descriptions of *gorgone* Larvae

Other larval descriptions of *gorgone* exist. Only shortly before the appearance of the paper by Edwards (1894), Dyar (1893) described what was apparently a rufa larva ("body brownish-red") although it might have been a variant bicolor as he further describes it "with a dorsal and subdorsal black shaded line." Handford (1933) described the diapausing behavior of *gorgone* larvae but he gave no phenotypic description. Leussler (1938-39) mentioned that the larvae of *gorgone* were easily reared but made no mention of larval phenotypes. Heitzman (1963) referred to the similarity of the "quite black" larvae of *Chlosyne nycteis* (Dbl.) to the larvae of *gorgone* without referring to the polymorphic nature of *gorgone* larvae.

One reference to the similarity of the larvae of *lacinia* and *gorgone* has been found. Cockerell (1914) described the bicolor and rufa of *gorgone* (as *Phyciodes ismeria* Bdv. & Lec.) from Boulder, Colorado. It is strange that the nigra morph was not also described as nigra is the most common morph in Kansas populations (Neck, 1974). Reference is made to the fact that the two morphs described for *gorgone* "nearly correspond to two varieties" of *lacinia*. The two morphs which Cockerell described are the same two which had been previously reported (bicolor by Edwards, 1894, rufa by Dyar, 1893). Apparently the trimorphic nature of the larvae of *gorgone* was not realized until the recent publication on the genetics of this polymorphism (Neck, 1973b).

Most general (Morris, 1862; Scudder, 1889:III, 1811; Holland, 1898, 1931; Klots, 1951) and regional (Macy and Shepard, 1941; Brown et al., 1957; Ebner, 1970; Harris, 1972) butterfly manuals repeated a description for *gorgone* which best fits a rufa larva but differs from the one above. This description originated from Boisduval and LeConte (1833:168) whose name *ismeria* is now relegated to a synonym of *gorgone* Hubner (see Dos Passos, 1969). The description refers to a larva which is "yellowish with three longitudinal black stripes." Edwards (1894) states that the description of *ismeria* larvae "has no application" to the *gorgone* larvae he reared.

This description, however, also closely fits the larva of *Chlosyne harrisii* (Scudder). The better fit of the larval description of *ismeria* may be significant in that the dispensation of this name has not been completely settled. Higgins (1960) felt that *ismeria* more closely resembles aberrant forms of *harrisii*. F. M. Brown (1974) felt that *ismeria* is a synthetic drawing, possibly a modification of *harrisii* or *gorgone*. The description of the larva gives some credence to the view that *ismeria* is some form of *harrisii* although a *harrisii-gorgone* hybrid is also a possibility. However, the supposed type locality of *ismeria*, Georgia, is more likely to be *gorgone* as *harrisii* is not presently known from localities that far south. A likely solution to this nomenclatural problem is that *ismeria* is an extreme form of *gorgone* as some contemporary *gorgone* are known from Georgia which closely resemble *ismeria* (Harris, 1972:264, color plate 7).

Reasons for Lack of Study

It can thus be seen that of the three people who described the larvae of *lacinia* in detail, only one (Cockerell in Edwards, 1893) divided the larval forms into three distinct categories. Apparently only one person (again Cockerell) saw more than one morph of *gorgone*. Comstock apparently saw all three morphs of *lacinia*, but he did not separate them into three distinct categories. This may have been partially due to the effect of environmental factors and/or genetic modifiers which tend to produce a nearly continuous variation from a basically discontinuous genetic polymorphism (Neck, 1974). Koehler, like Comstock, did not take notice of the three morphs of *lacinia*, although it appears that this larval polymorphism of color patterns is also present in Argentine populations.

The phenomenon of polymorphism was not as widely discussed at the times of the above descriptions as it is now. This may partially explain the lack of distinction between larval morphs of *lacinia*. At the time of most early descriptions of larvae of these species there was little concept of polymorphism in the United States scientific community. Mendel's work had not yet or had just become known; forms other than the supposedly ubiquitous "wild-type" were considered sports. Later, the rise of the ecological genetics school in England saw work on *Panaxia*, *Biston* and *Cepaea*. From this beginning polymorphism has become one of the most discussed biological phenomena of today.

Interestingly, one publication (Edwards, 1893) includes the term polymorphism in the title. Here, however, the term is applied to variant forms of the adult phenotypes of *lacinia* (*adjutrix* Scudder and *crocale* Edwards and hybrids thereof), not to the larval stages. At that time attention for studies was focused (as it still is today, although to a lesser extent) upon imaginal forms. Larval descriptions were recorded for identification purposes, but these stages were often considered to be merely a stage required to produce the adult form and not a form with its own adaptive strategy. Cockerell (1914) referred to the larvae of *lacinia* as "polychroic."

The descriptions in Edwards (1893) were not picked up by most later workers. Higgins (1960) does not refer to this paper in his discussion of the larvae of *lacinia* although he does refer to the paper in other contexts. Holland (1898) in his first edition refers to the larvae as being "fully described by Edwards"

and follows with the correct reference (Edwards, 1893), but he does not repeat the larval descriptions. For some unknown reason he drops the mention of this description in his revised edition (Holland, 1931) and says nothing of the larvae of *lacinia*. As most subsequent national and regional butterfly treatments are based upon this work, subsequent guides say nothing of the larvae of *lacinia*. The reference was not completely lost, however, as Davenport and Dethier (1937) in their bibliography of rhopaloceran life histories listed this reference with respect to *lacinia*.

The long, unprecise description of *lacinia* larvae given by Comstock (1927) would not likely be republished by workers who would prefer a short, precise description for publication in a guide book. As this description was published in a regional butterfly book, it would not have received the wide distribution of a book of the scope of Holland (1898, 1931). In his book, Comstock (1927) does not refer to the Edwards (1893) reference, although he does make reference to it in a later paper (Comstock, 1946).

The lack of study of these larvae may also be related to the non-occurrence of *lacinia* and apparent uncommon occurrence of *gorgone* in those areas extensively studied by the early American lepidopterists, i.e. the northeastern states. *C. lacinia* occurs from Texas westward to southern California and southward to Argentina. *C. gorgone* ranges from Texas to Manitoba, occurring into the eastern Rockies particularly along water courses. It is also sporadically reported throughout the southern states to Florida and Georgia. An apparently isolated population of *gorgone* occurring in northern New York is the only known eastern record north of Georgia (Shapiro, 1974).

Both butterflies are opportunistic species of varying abundance whose larvae feed upon species of the family Compositae which are characteristic of highly disturbed habitats (Neck, 1973a and unpublished data). Much of the ranges of these species includes areas which are characterized by long periods of dry weather when butterflies are essentially non-existent. This is particularly true of the desert and semi-desert areas of southern California, Arizona, New Mexico and western Texas. This fluctuating pattern of population size may possibly have contributed to their being overlooked. Edwards (1894) remarks on the lack of study as follows: "Considering what a common

species *carlota* is over at least one-third of the territory of the United States, it is remarkable that so little has been published respecting it." He further notes that some of his correspondents found this species to be common, while others in the same region found it rare.

As neither of these species is an agricultural pest, there was no study by agricultural scientists. Although both feed on wild sunflowers, the commercial monocephalic sunflowers are not readily acceptable to *lacinia* (Neck, 1973a).

SUMMARY

A striking polymorphism involving color polymorphism is exhibited by the larvae of *Chlosyne lacinia* and *Chlosyne gorgone*. These polymorphisms have remained unstudied until very recently because of a combination of factors. Their geographical ranges occur, for the most part, outside the areas most intensively studied by early American lepidopterists. A reference describing the polymorphic nature of one species was not utilized by later workers. Only recently was the complete polymorphic status of the other species described. Other descriptions referred to a single morph (in one case two morphs were described) or described a continuous variation of larval phenotypes. A problem of taxonomic nomenclature resulted in an erroneous description for *gorgone* in most butterfly texts. Characteristics of their population biology also tend to lessen the chances of study.

ACKNOWLEDGEMENTS

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THE BUTTERFLY FAUNAS OF SAN ANDRES AND PROVIDENCIA ISLANDS IN THE WESTERN CARIBBEAN

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SAN ANDRES ISLAND AND PROVIDENCIA ISLAND are the westernmost islands in the West Indies, lying only about 120 miles east of the Nicaraguan coast. Both islands are located beyond the 100 fathom level (Fig. 1), however, in the western Caribbean and there is no evidence for submerged banks between the islands and the mainland that might have supported butterflies or other organisms during a past period of lowered sea level (Corn and Dalby, 1973). Thus this isolated pair of islands and associated tiny cays are of considerable interest in considering the colonization and evolution of island butterflies in the West Indies, and despite excellent recent reviews of Antillean butterfly zoogeography (Scott, 1971, 1972), there has been no published survey of the San Andrés and Providencia butterflies.

In company with other faculty and students in the Organization for Tropical Studies, Inc. course program in Costa Rica, I was able to make five visits to these islands at various times in the dry and wet seasons of 1967 and 1968. I collected on San Andrés during March 25-26 and July 22-30, 1967, and February 19-23, June 21-24, and July 15-22, 1968; collecting on Providencia was done on June 2 and July 20-21, 1968. The records of butterfly species in this report come entirely from this collecting. Specimens are deposited in the Florida State Collection of Arthropods and the author's personal collection.

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DESCRIPTION OF THE ISLANDS

San Andrés and Providencia lie approximately 202 and 240 km, respectively, east of Nicaragua. For historical reasons, both islands are possessions of the country of Colombia. San Andrés ($120^{\circ} 35' \text{ N}$, $81^{\circ} 42' \text{ W}$), the more southerly of the two islands, is about 13 km long and 3 km wide. The relief is comparatively gentle, with a central hill rising to a maximum height of about 104 m (338 feet) above sea level. The island is completely covered by a layer of hard limestone, although underneath it is assumed to be basically volcanic. Several freshwater ponds (the largest of which is known as "Big Pond," placed at the island's center) are present. Most of the island is presently devoted to the cultivation of coconut palms and Colombian tourism, and the human population density is great (17,000 residents in 1967—distributed over the 16 square miles of island area). During the 17th and 18th centuries, however, there apparently were extensive natural stands of "cedar," possibly *Cedrela odorata* in the family Meliaceae (Whitmore and Hartshorn, 1969), which were decimated by the early colonists.

Providencia ($13^{\circ} 21' \text{ N}$, $81^{\circ} 22' \text{ W}$) is located about 88 km NNE of San Andrés and differs markedly from it in vegetation, topography and superficial geology. Approximately 8 km long and 5 km wide, it is a high, rugged island of andesite and basalt, with steep, rocky, central peaks rising to 363 m (1100 feet) above sea level. No freshwater ponds are found; however, several streams descend from the peaks. They may become intermittent during the dry season (January-April). In the higher regions of Providencia, bracken and tree ferns are common, and in the steeper uncleared areas occur dense thickets of figue (*Fourcroya* sp.), calabash (*Crescentia* sp.), and other trees. Coconut palms are found only infrequently, and there are few agricultural areas; introduced guinea grass (*Panicum maximum*) supports some cattle in the lower valleys. Extensive mangrove swamps occupy a considerable portion of the northeast shore. Few tourists visit this island, the transportation being infrequent and the facilities minimal.

The climate on both islands is tropical, with the average daily temperature being about 27°C throughout the year. The dry season, as in Central America, lasts from January to April, March and April being the driest months. October and November are normally the wettest months. The average annual rainfall on San Andrés between 1934 and 1943 was 1824 mm (71.81 inches).

The interglacials of the Pleistocene Epoch would have considerably decreased the surface area of low-lying San Andrés. The glacial periods, however, clearly greatly modified the surface areas of both islands, as indicated by the extensive and massive coral reefs and shoals bordering parts of each island. Providencia lies 74 km, and San Andrés 83 km, from the 100 fathom depth line off mainland Central America. Soundings of trenches as deep as 1500 m have been taken between the two islands.

THE BUTTERFLIES OF SAN ANDRÉS

Fifteen species of butterflies were taken or observed on this island. Most were distributed generally around the island, as were the seven species of dragonflies recorded earlier by Paulson (1968). No Papilionidae, Satyridae, Libytheidae, Riodinidae, or Megathymidae were found. It is strange that *Heliconius charitonius* and *Euptoieta hegesia* are apparently absent. A list of recorded species follows.

DANAIDAE

1. *Danaus plexippus* Linnaeus.

Scattered and relatively worn individuals were seen on all dates. No milkweeds were seen on this island.

NYMPHALIDAE

1. *Dryas julia* Fabricius.

A number of subspecies of this long-winged heliconian have been named from various Caribbean islands (and mainland areas), for the species seems to vary distinguishably from island to island (see Brown and Heineman, 1972, for a partial review). No special name is presently assigned to the San Andrés-Providencia populations.

Dryas flies in fair abundance on the slopes around Big Pond throughout the year and is continuously brooded here and elsewhere on San Andrés with fresh adults appearing every month. *Dryas* is relatively rare at Puerto la Ensenada, on the central west coast of San Andrés. On 21 February 1968, two *Dryas* males were observed courting different *Agraulis vanillae* females around 0900 and 0915 hours, in low second-growth vegetation. Female *Dryas* have a dark blackish band across the forewings, while males rarely have any indication of this band.

2. *Agraulis vanillae* Linnaeus.

Rare in the Big Pond area (where *Dryas* is abundant), the Gulf Fritillary is quite abundant at Puerto la Ensenada on the west coast (24 adults in an hour in February). It resembles typical Florida *A. v. nigrrior*, although the black forewing spots often form a bar-like continuous row. Young larval instars were found on *Passiflora* sp. at the Puerto area.

3. *Victorina (Siproeta) stelenes* (Linnaeus).

Several fresh specimens were observed (Big Pond area, Hotel Casa Blanca) each day in February, but it was rarer in other months. The species is known to feed on *Blechnum blechnum* and *Ruellia coccinea* (Acanthaceae) in Jamaica (Brown & Heineman, 1972); these are weedy plants which may well occur on San Andrés.

4. *Historis odius* Fabricius.

A robust, strong-flying nymphalid, *Historis* is a rare sight on San Andrés (July 1967, 1968) but its black and orange-brown coloration is unmistakable. The few adults seen may be strays from Providencia or even the mainland because its only known foodplants are trees of the genus *Cecropia*, a member of the Urticaceae and characteristic inhabitant of lowland rain forest areas in the New World tropics.

5. *Precis evarete zonalis* Felder & Felder.

The West Indian buckeye is a medium-sized dark brown butterfly with small hindwing ocelli. It also occurs on the mainland from northern Mexico and the southern tip of Florida south to Venezuela and Trinidad. It is relatively rare on San Andrés and occurs principally in the Big Pond area (February, July).

6. *Anartia jatrophae* Johansson.

This nymphalid is quite variable through its Neotropical range, and the species also shows seasonal variation in color and pattern. It prefers weedy areas and is fairly common in July, but rare in February.

PIERIDAE

1. *Phoebis sennae sennae* (Linnaeus).

This large, rich yellow Cloudless Sulphur has scattered patches or lines of reddish brown scales on the underside of the hindwing. Fresh specimens were seen daily, but

the species is not particularly common in February, March or July. A low-growing weedy *Cassia* (larval foodplant) is found on the coastal margins and around Big Pond.

2. *Eurema daira* Godart.

This variable *Eurema*, common in the Antilles and on the mainland in Nicaragua and Costa Rica, is relatively rare on San Andrés; it was recorded daily in July but not in February. The larvae feed elsewhere on vetches and other related Fabaceae. The species is known to be migratory in Costa Rica.

3. *Eurema lisa* Boisduval & Leconte.

The Little Sulphur is also comparatively rare on San Andrés and was noted only during the wet season in July (T.C.E., G. N. Ross). Its larval host are *Mimosa* and *Cassia*; both present on San Andrés.

LYCAENIDAE

1. *Leptotes cassius* (Cramer).

A very common blue throughout the West Indies, this *Leptotes* is quite colonial on San Andrés. A large population exists slightly north of Puerto la Ensenada, centered around low beach legumes, while none were found at Big Pond or around the settlements with the exception of one male seen visiting flowers at the Hotel Casa Blanca.

HESPERIDAE

1. *Urbanus proteus* (Linnaeus).

This dark long-tailed skipper, with iridescent greenish-blue wing-scaling near and on the thorax, is common on the island and the adjacent mainland. Gravid females with mature eggs were found in both February and July at Big Pond, where the species was using unidentified low-growing legumes as larval hosts.

2. *Pyrgus oileus* (Linnaeus).

The former name of this common checkered skipper in the Caribbean was *P. syrichtus* (Brown & Heineman, 1972). *Pyrgus oileus* was seen sporadically around Big Pond (February 1968).

3. Small brown skipper, possibly female *Hylephila phyleus* (see Providencia list).

One was seen but not captured, along road above the east side of Big Pond on 22 February 1968.

4. Small black skipper (body length 9 mm).

One specimen was taken in a sweeping study of grass-inhabiting insects under coconut palms, near the trail going up from the east side of Big Pond, at 1000 hours on 22 February 1968. Unfortunately, it was so damaged by debris in the sweep net that identification was impossible.

THE BUTTERFLIES OF PROVIDENCIA

Local inhabitants suggested that butterflies on this island were at their peak later in the wet season than when collecting was done in the present study (June and July). From personal observation, I would agree that the flight peak for resident species is probably more marked than on San Andrés and that good population numbers likely do not appear until August through October or November. Every species found on San Andrés also must occur on Providencia, and with the greatly increased diversity of vegetation on Providencia, one would presume that several additional species of butterflies should occur. The discovery of a second *Phoebis* species and another skipper species, even with very little sampling time, supports this view. Most of the records reported here were obtained on the southern and western coastal and moderate-elevation areas.

DANAIDAE

1. *Danaus plexippus*.

NYMPHALIDAE

1. *Dryas julia*.
2. *Agraulis vanillae*.
3. *Historis odius*.

PIERIDAE

1. *Phoebis sennae*.
2. *Phoebis statira* Cramer.

A large *Phoebis* with the basal two-thirds of the wing yellow and the outer third covered with whitish scaling, *P. statira* is a pandemic species in the Caribbean area and its migratory behavior is well known. Though only two males were seen in July, the presence of its *Cassia* food-plants likely means it is a breeding resident on at least Providencia if not also on the more arid island of San Andrés.

LYCAENIDAE

1. *Leptotes cassius*.

HESPERIIDAE

1. *Hylephila phyleus phyleus* (Drury).

The Fiery Skipper is found throughout the West Indies and North, Central, and South America. It is common on Providencia in lush grassy areas from sea level to over 800 feet elevation.

DISCUSSION

A total of 17 species of true butterflies and skippers were found on San Andrés and Providencia Islands, located about 120 miles east of the coast of Central America. No endemic species occur on these isolated West Indian islands, nor are there any uniquely Antillean residents. All of the butterflies are also found on the adjacent Nicaraguan mainland area, and all represent species that are migratory or are known to be frequent colonizers. This situation is typical of the Antilles as a whole, where more than 60 percent of the relatively impoverished butterfly fauna of 285 species are widespread continental species of great dispersal ability (Scott, 1971, 1972). Further collecting in the high interior of Providencia and during the wet season will undoubtedly uncover several additional resident species of butterflies and skippers.

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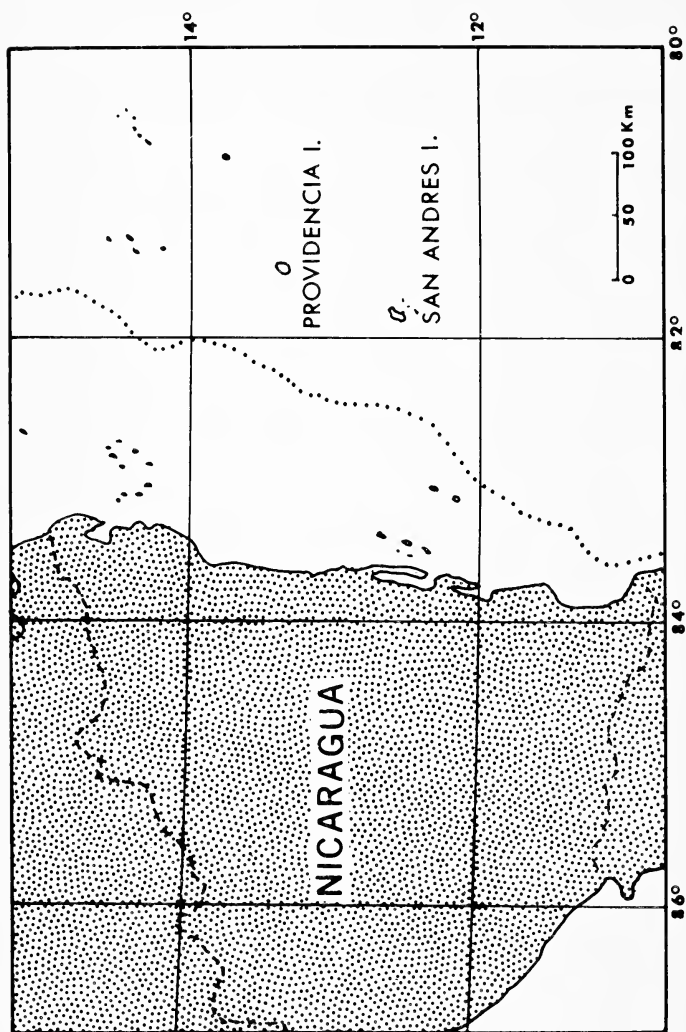


Fig. 1.—The position of San Andrés and Providencia Islands, Colombia, in the western Caribbean in relation to Nicaragua on the mainland of Central America. The 100-fathom depth level of the ocean is indicated by a dotted contour line.

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A LIST OF THE BUTTERFLIES OF THE WILLOW RIVER STATE PARK, WISCONSIN

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8126 Santa Inez Drive, Buena Park, California

WILLOW RIVER STATE PARK, in Saint Croix County, northwest Wisconsin, was officially opened in 1972 and is the newest addition to the Wisconsin state park system. The Park consists of three small impounded lakes on the Willow River, recreational areas that are for the most part adjacent to these lakes and several hundred undeveloped acres of woodland, meadows and old pastures. It is a very good area for the collection and study of Lepidoptera.

I previously listed (Masters, 1973) 42 species of butterflies as occurring in St. Croix County where I resided for 3 years. Heavy collecting in the Willow River Park has added 7 species to the county list and 12 species of Hesperidae (not included in the previous list) were also observed, making a total of 61 species taken in the State Park or its immediate vicinity. The large number of species taken here is a result of the diverse habitats available in the Park which include deciduous woodland, both wet and dry meadows, remnant prairie and oak openings. A list of the species taken follows:

HESPERIOIDEA

Poanes hobomok (Harris)

Atrytone delaware (Edwards)

Wallengrenia otho (Smith)

Polites coras (Cramer)

Polites themistocles (Latreille)

Polites mystic (Scudder)

Hesperia metea Scudder

Erynnis icelus (Scudder & Burgess)

Erynnis juvenalis (Fabricius)

Pyrgus communis (Grote)

Ancyloxypha numitor (Fabricius)

Epargyreus clarus (Cramer)

PAPILIONOIDEA

- Papilio polyxenes asterius* Stoll
Papilio glaucus glaucus Linnaeus
Pieris protodice protodice Boisduval & LeConte
Pieris rapae rapae (Linnaeus)
Colias eurytheme eurytheme Boisduval
Colias philodice philodice Godart
Colias interior interior Scudder
Colias cesonia cesonia (Stoll)
Nathalis iole Boisduval
Euchloe olympia olympia (Edwards)
Libythea bachmanii bachmanii (Kirtland)
Danaus plexippus plexippus (Linnaeus)
Lethe anthedon anthedon (Clark)
Lethe eurydice eurydice (Johansson)
Euptychia cymela cymela (Cramer)
Cercyonis pegala nephele (Kirby)
Asterocampa celtis celtis (Boisduval & Le Conte)
Limenitis arthemis/astyanax (Fabricius) hybrid population
Limenitis archippus archippus (Cramer)
Vanessa atalanta rubria (Fruhstorfer)
Cynthia virginiensis (Drury)
Cynthia cardui (Linnaeus)
Nymphalis milberti milberti (Godart)
Nymphalis antiopa antiopa (Linnaeus)
Polygonia interrogationis (Fabricius)
Polygonia comma (Harris)
Polygonia progne (Cramer)
Phyciodes tharos tharos (Drury)
Chlosyne nycteis nycteis (Doubleday)
Boloria selene nr. myrina (Cramer)
Boloria bellona bellona (Fabricius)
Speyeria idalia (Drury)
Speyeria cybele cybele (Fabricius)
Speyeria aphrodite aphrodite (Fabricius)
Speyeria aphrodite alcestis (Edwards)
Euptoieta claudia claudia (Cramer)
Harkenclenus titus titus (Fabricius)
Satyrium edwardsii (Grote & Robinson)
Satyrium calanus falacer (Godart)
Satyrium caryaevorus (McDunnough)
Satyrium acadica acadica (Edwards)

Incisalia henrici henrici (Grote & Robinson)
Mitoura gryneus gryneus Hubner
Feniseca tarquinius tarquinius (Fabricius)
Lycaena xanthoides dione Scudder
Lycaena helloides (Boisduval)
Lycaena phlaeas americana Harris
Glaucopsyche lygdamus couperi Grote
Everes comyntas comyntas (Godart)
Celastrina argiolus pseudargiolus (Boisduval & Le Conte)

Satyrrium caryaevorus, which is new to the county list, seemed to be restricted to Oak Opening communities and seemed to fly much higher up in the oak and hickory trees than *Satyrrium calanus* which flew with it. *Speyeria idalia* actually did not occur in the state park, but was taken on a patch of remnant prairie along a railway track just south of the park. *Colias interior* was recorded from a single male (very definitely this species) that was taken at the edge of a field of cultivated strawberries on the south border of the park!

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LIVE GEOMETRID

(Cover illustration)

NOEL McFARLAND

P. O. Box 475, Geraldton, W. Australia 6530

Both upper and lower photos show the same moth, at rest, as viewed from two different angles. No leg or wing movements have taken place.

Identification: *Oenochroma vinaria* Guen.

(N. McF. code No. G. 77)

Family GEOMETRIDAE—Subfamily OENOCHROMINAE

Locality: South Australia, Mt. Lofty Range, nr. Blackwood. July 30 1967, 0200 hrs. at UV light, Noel McFarland

Photographed by Noel McFarland.

Lower figure: Living adult ♂ in its natural position, as viewed from the rear. Right antenna visible tucked along side of the thorax, beneath wings. Length of forewing, from base to tip is 24 mm. This species normally rests on litter or near the ground among dead leaves; thus, the wings are held up at rest rather than appressed to the substrate. The uplifted wings cast a shadow as do the variously twisted and bent dead leaves.

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

C O N T E N T S

Volume 13 Number 1 March, 1974

Studies on Nearctic <i>Euchloe</i> — Part 7	Paul A. Opler	1
3 Stacks of the eggs of <i>Hemistola hatching</i>	Noel McFarland	21
Checklist of the Macroheterocera of south-eastern Ontario	P. S. Ward, R. Harmsen, and P. D. N. Hebert	23
A new species of <i>Hypagyrtis</i>	Roger L. Heitzman	43
Genetic control of maculation and hindwing color in <i>Apantesis phalerata</i>	Jack S. Bachele and Thomas C. Emmel	49
Natural and laboratory occurrence of "Elymi" phenotypes in <i>Cynthia cardui</i> (Nymphalidae)	Arthur M. Shapiro	57
Das naturhistorische Museum in Wien und seine Lepidopterensammlung	Dr. Fritz Kasy	63
Notice	William Hovanitz	66
Habitat: <i>Adela bella</i> in Florida	John B. Heppner	67

Volume 13 Number 2 June, 1974

The butterfly fauna of the Sacramento Valley, California	Arthur M. Shapiro	73
Extended flight periods of coastal and dune butterflies in California	Robert L. Langston	83
Habitat: <i>Brephidium pseudofea</i> (Lycaenidae)	John B. Heppner	90
The early stages of various species of the genus <i>Dirphia</i> (Saturniidae)	Brian O. C. Gardiner	101
A new species of <i>Orniseodes</i> (<i>Dirphiella</i>) from Mexico (Saturniidae: Hemileucinae)	Julian P. Donahue and Claude Lemaire	123

A new subspecies of <i>Euphydryas editha</i> from the Channel Islands of California	Thomas C. Emmel and John F. Emmel	131
--	-----------------------------------	-----

<i>Volume 13</i>	<i>Number 3</i>	<i>September, 1974</i>
------------------	-----------------	------------------------

Studies of the ova and first instar larvae of Geometridae (Ennominae). I.	Roger L. Heitzman	149
Altitudinal migration of central California butterflies	Arthur M. Shapiro	157
The chromosomes of <i>Apantesis phalerata</i> , <i>A. radians</i> , and their hybrid in Florida populations (Arctiidae)	Jack S. Bacher and Thomas C. Emmel	162
A partial bibliography of the world distribution and zoogeography of butterflies	Oakley Shields	169
The nomenclature in an important British checklist (1972) Part 2: Corrections of family-group names for Geometridae (Lepidoptera)	Juraj Paclt	179
Illustrations and descriptions of species of some Pyrrhopyginae from Panama (Hesperiidae)	S. S. Nicolay	181
Butterflies of the Suisun Marsh, California	Arthur M. Shapiro	191

<i>Volume 13</i>	<i>Number 4</i>	<i>December, 1974</i>
------------------	-----------------	-----------------------

Toward a theory of butterfly migration	Oakley Shields	217
<i>Atrytonopsis hianna</i> biology and life history in the Ozarks	J. Richard and Roger L. Heitzman	239
Larval migration of <i>Hyles lineata</i> (Fab.)	James F. Wells and Richard M. Brown	246
New food plant for <i>Darapsa pholus</i> (Cramer)	J. C. E. Riotte	247
Notes on Arctic and Subarctic collecting	Clifford D. Ferris	249
Kloet and Hincks' Check list of British Lepidoptera Insects (Lepidoptera) Edn. 2. A reply to criticisms J. D. Bradley, D. S. Fletcher and P. E. S. Whalley		265
The Nomenclature in an Important British check list (1972). Part 3. Correct gender for generic names derived from classical without change of termination	Juraj Paclt	267
Artificial Diet: The key to the mass rearing of <i>Megathymus</i> larvae	Ronald S. Wielgus	271
Review: Butterflies of the World by H. L. Lewis	Clifford D. Ferris	278

NOTICES

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IN THIS ISSUE

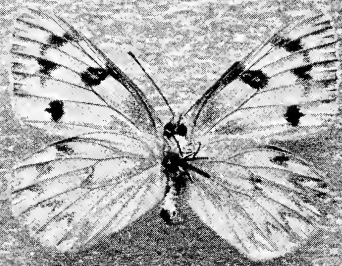
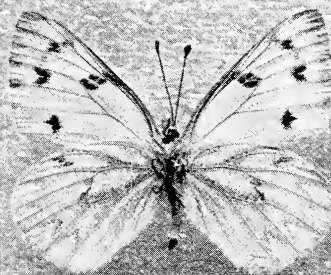
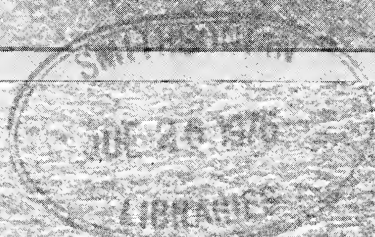
- | | | |
|---|-----------------|----|
| Mate-locating behavior of the
western North American butterflies | James A. Scott | 1 |
| History of scientific study on
a larval color polymorphism in
the genus <i>Chlosyne</i> (Nymphalidae) | Raymond W. Neck | 41 |
| The butterfly faunas of San Andres and
Providencia Islands in the western Caribbean | Thomas C. Emmel | 49 |
| A list of the butterflies of the Willow River
State Park, Wisconsin | John H. Masters | 57 |
| Live Geometrid | Noel McFarland | 60 |

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OF RESEARCH
ON THE LEPIDOPTERA.

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THE GENETICS OF SUBSPECIFIC PHENOTYPE DIFFERENCES

IN *PIERIS OCCIDENTALIS* REAKIRT AND OF VARIATION
IN *P. O. NELSONI* W. H. EDWARDS (PIERIDAE)

ARTHUR M. SHAPIRO

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THE WESTERN WHITE, *Pieris occidentalis* Reakirt, has one of the widest latitudinal ranges of any nearctic butterfly—from near 36°N above 3000 m in the White Mountains of Mono and Inyo Counties, California to 69°N at sea level at Umiat, Alaska. The northernmost population to be studied biologically is located at Fairbanks, Alaska (64°49' N); its bionomics are described in Shapiro (1975a) and its phenotypic and developmental responses to photoperiod in Shapiro (1975b). This population corresponds to the taxon *Pieris nelsoni* W. H. Edwards (type locality St. Michael, Alaska), characterized phenotypically by a reduced black pattern dorsally in the male as compared with nominate *P. occidentalis* from California or Colorado (figs. 1, 2). *Pieris nelsoni* was described from a single male in 1883 and then "lost" for 91 years; during which time its female remained unknown along with its degree of relationship to *P. occidentalis*. Following its rediscovery at Fairbanks, *P. nelsoni* was reared in quantity for photoperiodism studies, which revealed a longer-day threshold for diapause induction and a reduced propensity to produce the estival phenotype (lightly marked ventrally) as compared with *P. occidentalis* (Shapiro, 1975b). However, its early stages were indistinguishable from *occidentalis* and the pattern of the female differed from that taxon only very subtly. These facts suggested strongly that *nelsoni* and *occidentalis* were geographic subspecies of a single species, an hypothesis tested by the crosses reported below.

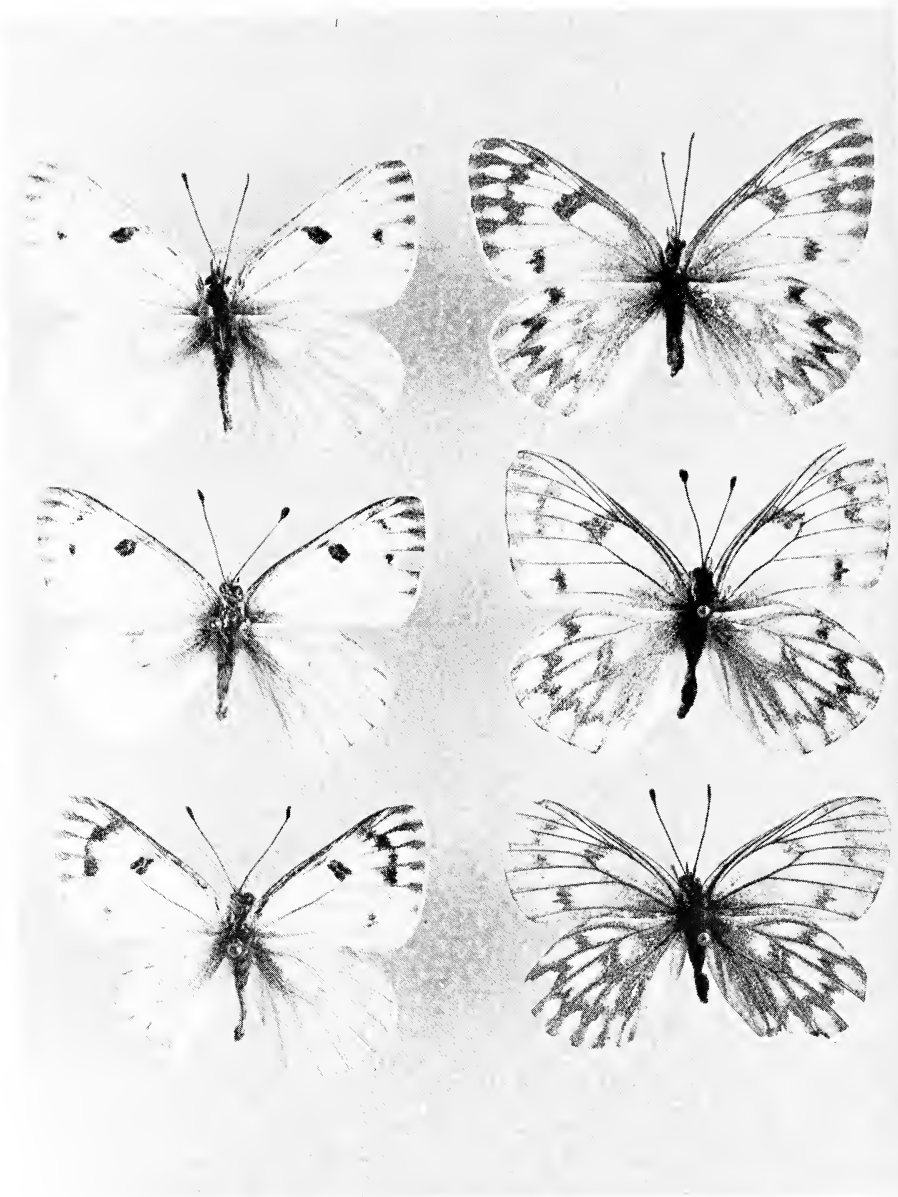


Fig. 1a.—Dorsal surfaces of wild *Pieris occidentalis nelsoni* from Fairbanks, Alaska, July 1974. Males at left.

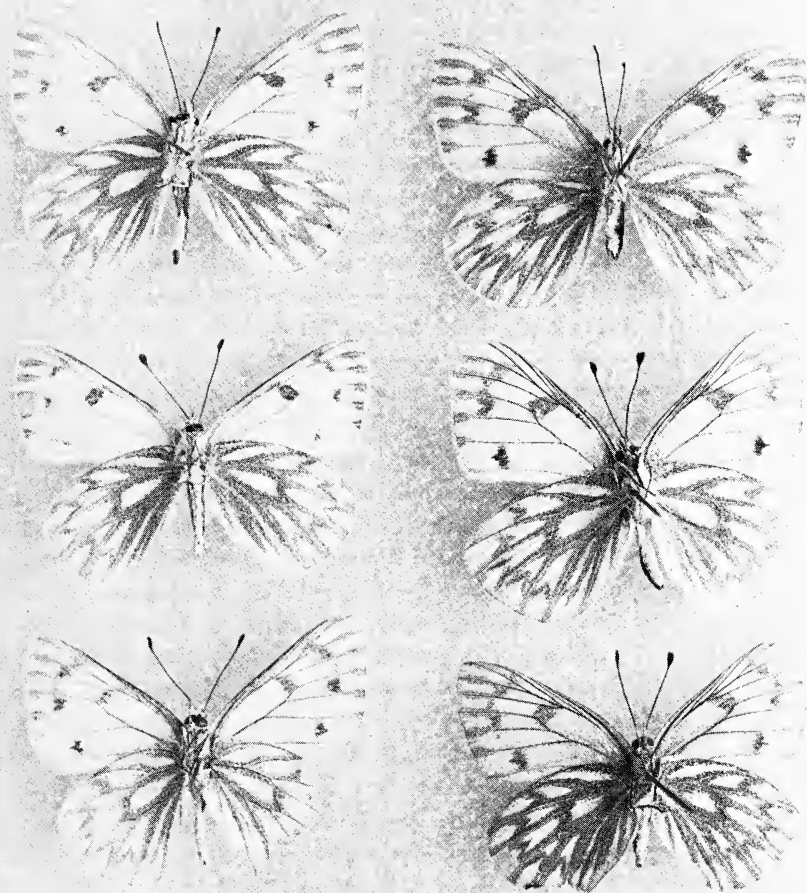


Fig. 1b.—Ventral surfaces of same.

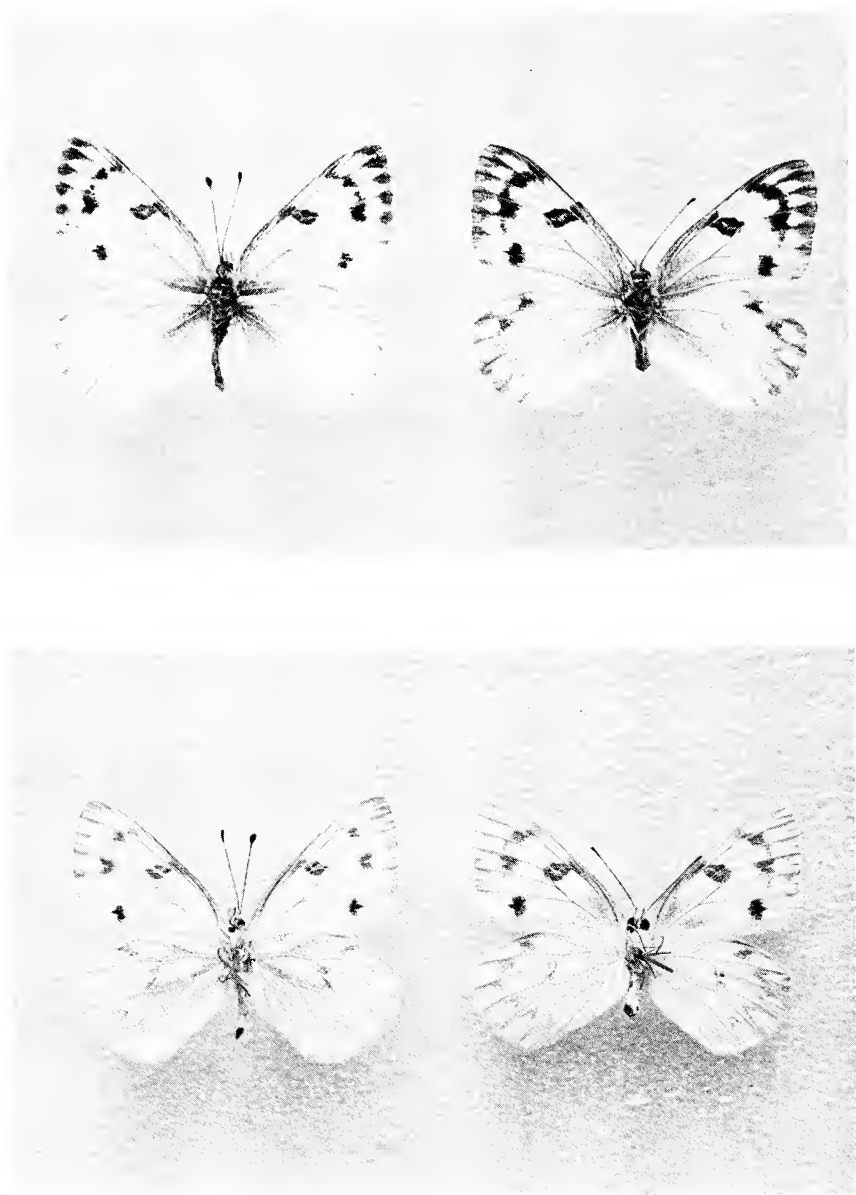


Fig. 2.—Dorsal and ventral surfaces of wild *Pieris occidentalis* from Donner Pass, California. Males at left.

In breeding *P. nelsoni* from Fairbanks I obtained a number of aberrant individuals which were mated and studied in continuous culture. These are described, figured, and discussed elsewhere in this paper.

MATERIALS AND METHODS

The initial cross of Alaskan and Californian stocks was made using a fresh wild male *P. occidentalis* collected at 3000 m at the base of Sonora Peak, Mono County, California on 8 August 1974 by S. R. Sims. This male was caged with two virgin female *P. nelsoni* of the first generation in continuous culture, ex Fairbanks. This stock was maintained at 25°C under continuous light and reared on fresh *Lepidium virginicum* L. (Cruciferae). The wild male was not very vigorous but did mate with one female on the second day, and this female laid 8 eggs, of which 5 hatched. All of these eventually pupated, but two subsequently died, producing an F₁ of only three individuals—two males and a female. A sib mating was, however, obtained, producing 49 ova of which 40 hatched, yielding 37 pupae and 25 adults of the F₂.

All rearing was done in colorless plastic Petri dishes (diameter 14 cm) on *L. virginicum* at densities of 10 larvae or less/dish at 25°C under a 60-W incandescent lamp. They pupated in the dishes, and only non-diapause pupae were obtained. Eclosion took place in nylon-mesh cages 41 cm x 41 cm x 41 cm, and matings were obtained in these in filtered sunlight. All adults used for breeding were provided fresh dandelions as a nectar source. Mated females were confined in colorless plastic cages 19 x 13 x 10 cm with fresh cuttings of *Lepidium* and fresh dandelions and allowed to oviposit.

RESULTS OF HYBRIDIZATION

The F₁ consisted of two males, both intermediate between estival and vernal phenotypes, with complete *occidentalis* pattern, and one female with a dark-intermediate ventral pattern and a dorsal *occidentalis* pattern which, however, resembled *nelsoni* in having the spot at the end of the cell of the forewing narrow. All of these individuals became too battered to be figured.

The F₂ (figs. 3, 4) of 13 males and 12 females was exceedingly variable in all phenotypic characters, with seemingly independent assortment at several genetic loci. Within each sex, the

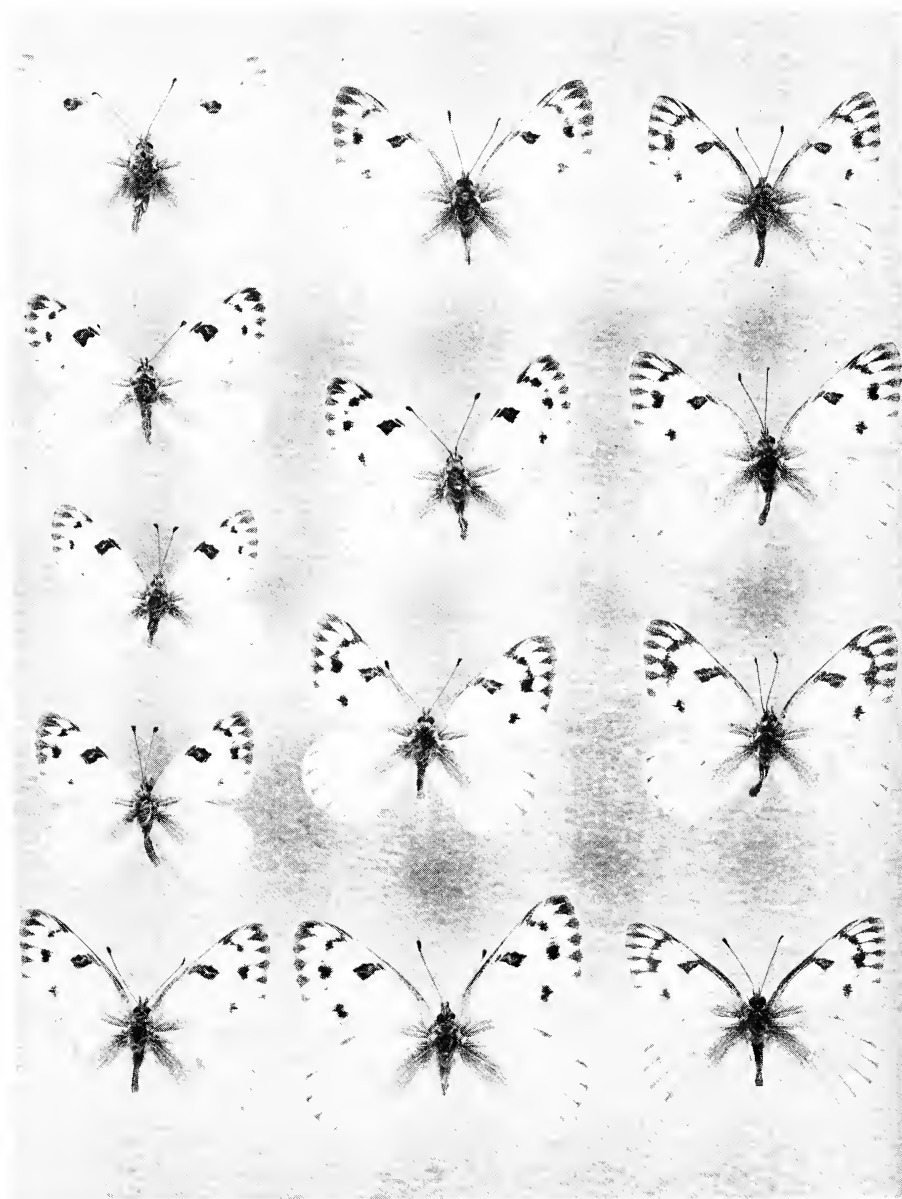


Fig. 3a.—Dorsal surfaces of F_2 males, Alaska X California *Pieris occidentalis*, reared at 25°C on continuous light.

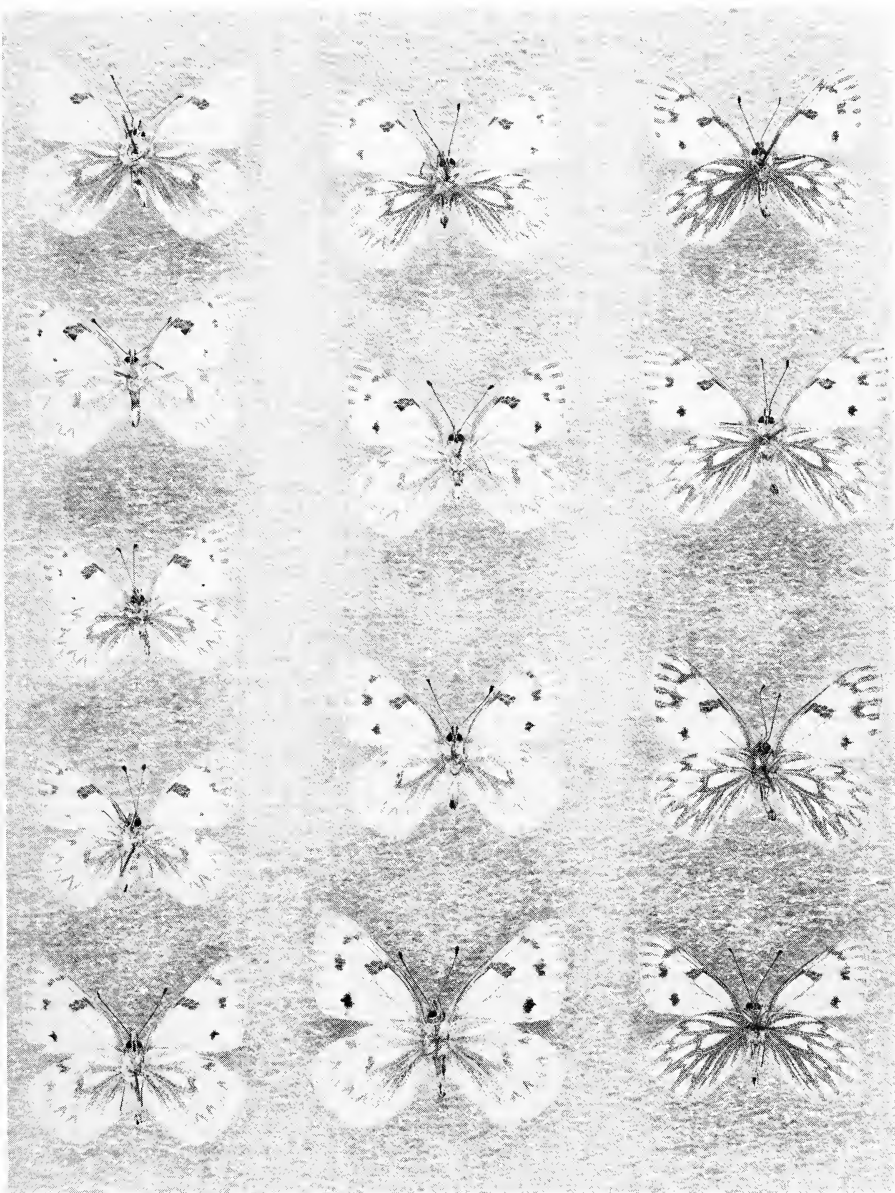


Fig. 3b.—Same but ventral.

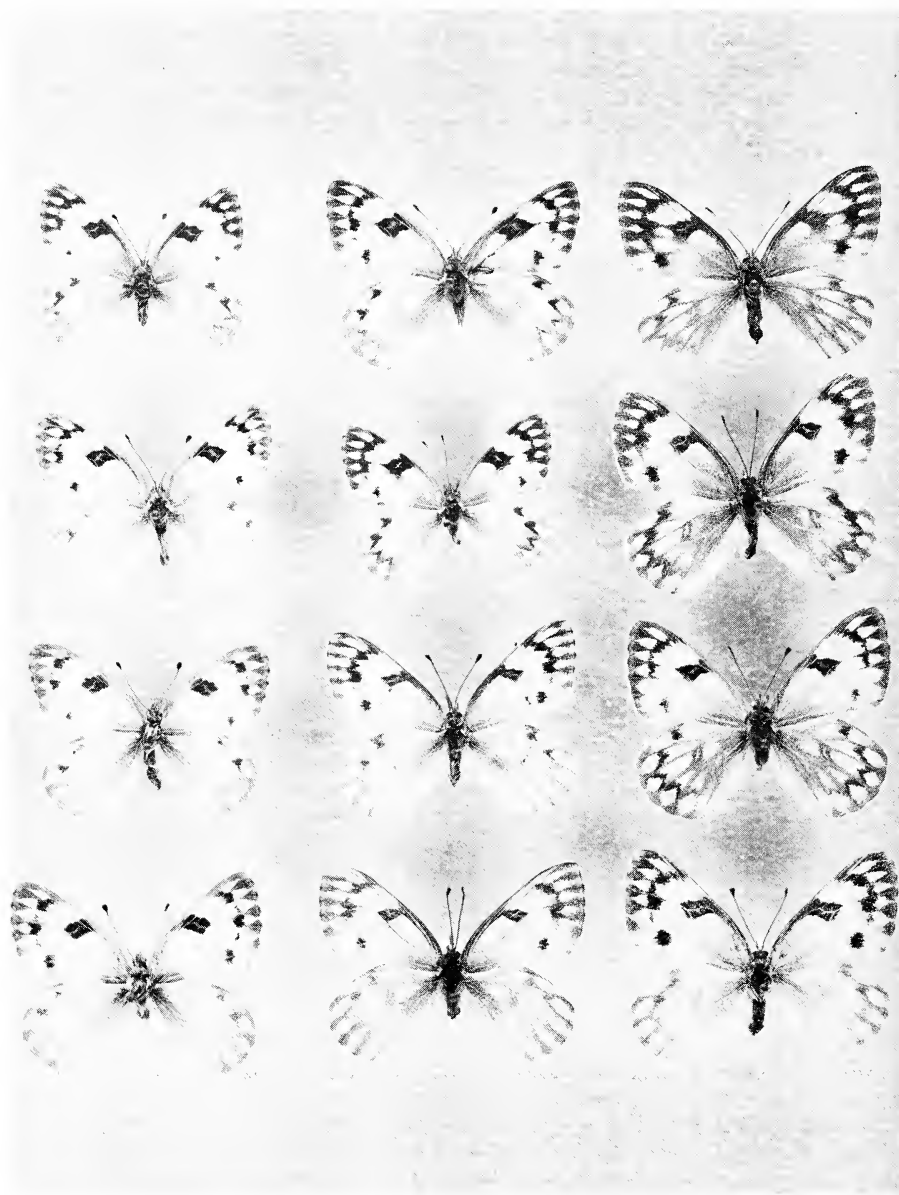


Fig. 4a.—Dorsal surfaces of F_2 females, Alaska X California *Pieris occidentalis*, reared at 25°C on continuous light.

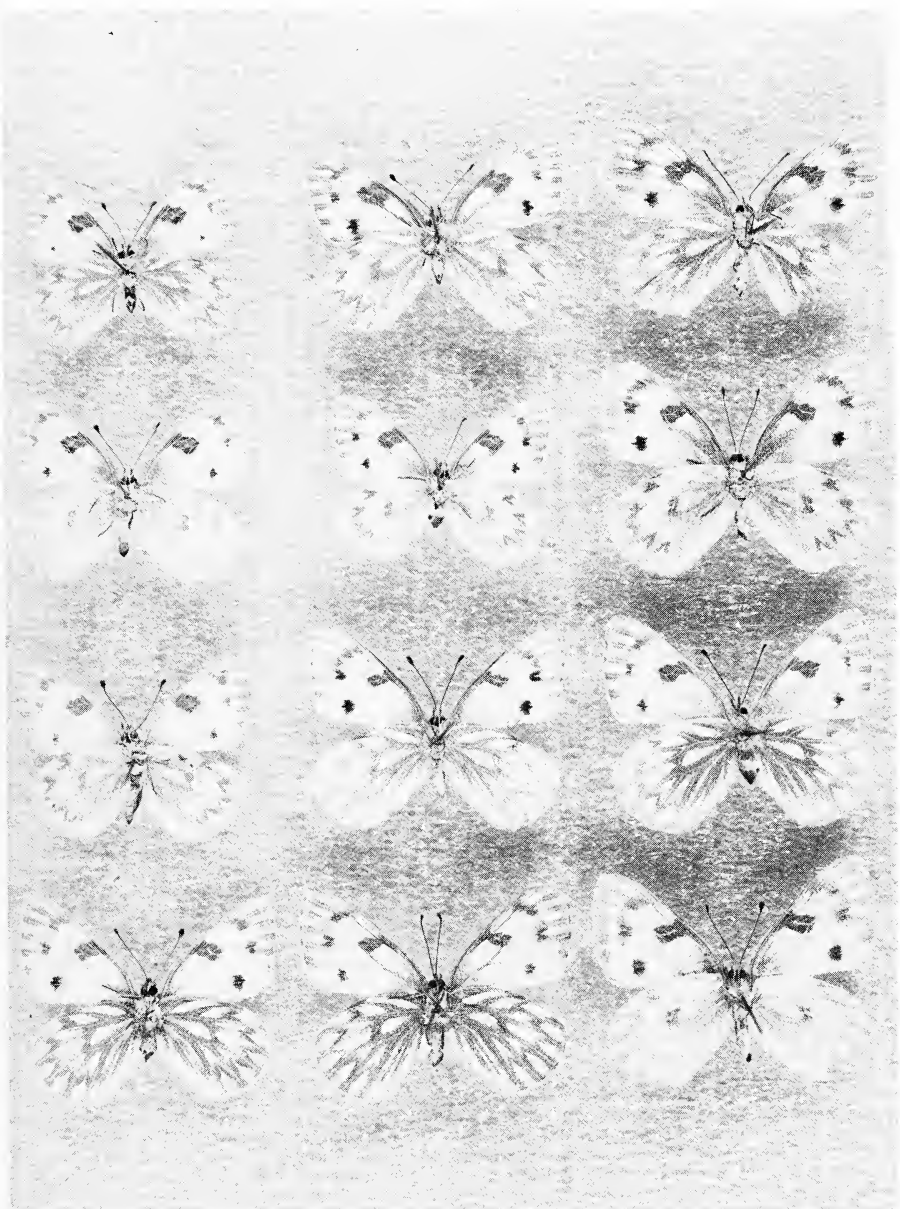


Fig. 4b.—Same but ventral.

phenotypic range includes apparently normal *occidentalis* and *nelsoni*, plus recombinants never seen in wild samples or pure bloods of either. Because of the small numbers of animals and the impracticability of large-scale genetic experimentation with these traits, only a very rough idea of their inheritance can be given. The traits which appear to be segregating are:

(1) *Dorsal pattern of male*. In *nelsoni*, the apical and sub-apical pattern elements are suppressed. This phenotype appeared only in one male of the F_2 , but several others had these black markings smaller than most male *occidentalis*. The sample is too small to discriminate between control by one locus, with the *nelsoni* allele recessive (expectation $1/4$ *nelsoni*), and two loci (expectation $1/16$ *nelsoni*).

(2) *Size and shape of spot in discal cell of forewing*. This trait is variable in both parental populations. The most frequent *nelsoni* state is "narrow" in both sexes; "narrow" is, however, rare in pure *occidentalis*. "Narrow" spot appeared in the F_1 female and in four males and four females of the F_2 . The males included the one with *nelsoni* dorsal pattern.

(3) *Dorsal pattern of female*. *Nelsoni* females do not differ from California *occidentalis* in any conspicuous character. They are more likely to have the black chevrons between the veins of the hindwing darker than the remainder of the pattern; the forewing more often has a complete (although narrow) black outer margin, and the white spots enclosed in the forewing border are usually broader in *nelsoni* than in *occidentalis*. The spot in cell Cu_2 is almost always smaller in female *nelsoni* and is occasionally lacking. In the F_2 , all of these characters are very variable. In three F_2 females and in the one F_1 female, the forewing border is broader than in either parental population, producing very elongate, narrow white spots enclosed within it. In five of the 12 F_2 females, the spot in cell Cu_2 is reduced as in *nelsoni*; in three it is heavier than in the average *occidentalis*. Both parental populations are variable as to basal dark shading, as is the F_2 . Control of female pattern is probably multifactorial and not an expression of the same major gene(s) involved in the male phenotypic difference.

(4) *Seasonal Phenotypes*. As noted in Shapiro, 1975b, *nelsoni* produces an estival phenotype (light ventrally), less often than does *occidentalis* when reared under continuous light. Again, the F_2 is extremely variable, and the variation is poorly correlated with characters on the dorsal surface. On the whole,

ventral melanization in both sexes in the F_2 is more similar to *nelsoni* than to Sierran *occidentalis*. In *nelsoni*, there is a tendency for the heaviest melanization to be basal, and this is found in four males and one female of the F_2 . One of the males is the single individual with dorsal *nelsoni* phenotype.

One F_2 female is asymmetrical. This female was not recognized as abnormal until after her death, but her phenotype is essentially identical to the trait "bilateral" previously found in Pennsylvania-New Jersey stock of the closely related species, *Pieris protodice* Boisduval and LeConte (Shapiro, 1970). This trait is inherited as an autosomal recessive. Some of the modifications produced in the homozygous "bilateral" *protodice* are related to the "ray" phenotypes discussed below.

ABNORMAL PHENOTYPES

The Fairbanks stock of *P. nelsoni* was started with five wild females, whose ova were pooled. In the F_1 , a number of aberrant individuals of both sexes were obtained, and several matings set up among them. The aberrant phenotype is apparently inherited as a simple autosomal dominant. It is expressed in both long- and short-day (estival and vernal) phenotypes (figs. 5, 6). Its differences from "wild type" are: Males: The submarginal black markings on the dorsal forewing are even more reduced than in "wild type" *nelsoni*, but the marginal triangles are present and may be slightly enlarged. The spot in cell Cu_2 is always absent and that at the end of the cell is slightly enlarged. Ventrally, the basal markings are more heavily melanized on the hindwing than "wild type" but the submarginal chevrons are only very weakly indicated. The spot at the end of the hindwing cell ventrally is enlarged. Females: The submarginal elements of the dorsal pattern are more or less reduced; as a minimum, the chevrons on the hindwing are not darker than the rest of the pattern and are thinner than in "wild type" *nelsoni*, making the enclosed white spots appear larger than normal; in estival-phenotype females the chevrons are usually obsolete. The spot at the end of the cell of the forewing is conspicuously enlarged (and ventrally may be prolonged basad along the cubitus, but not as a ray actually reaching the base). As in males, the basal melanization is exaggerated on the ventral hindwing.

In each of the six broods involving this phenotype reared in this study, a few highly abnormal individuals appeared in which the characters described above were exaggerated, along with distortion of the wing shape and (often) a reduction in

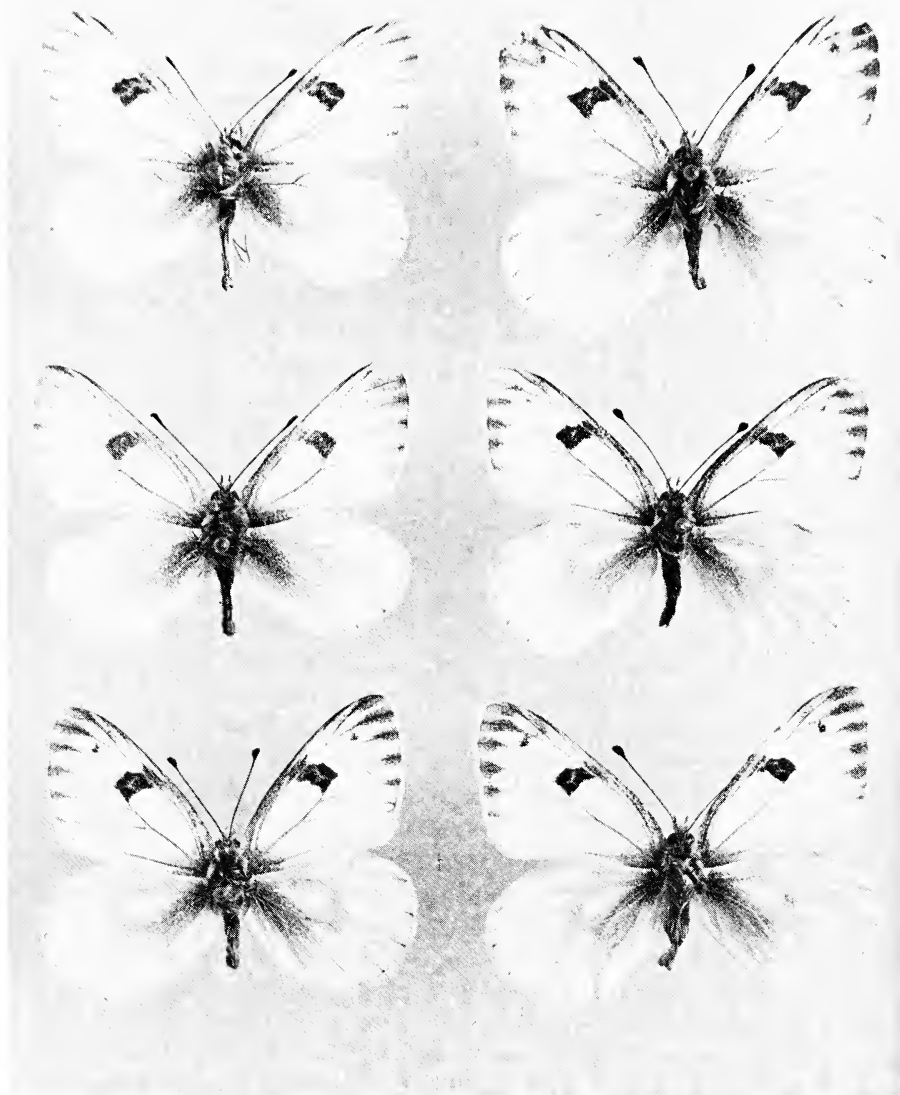


Fig. 5a.—Aberrant phenotypes of male *Pieris occidentalis nelsoni*, dorsal surfaces, illustrating light (estival) and dark (vernal) pattern.

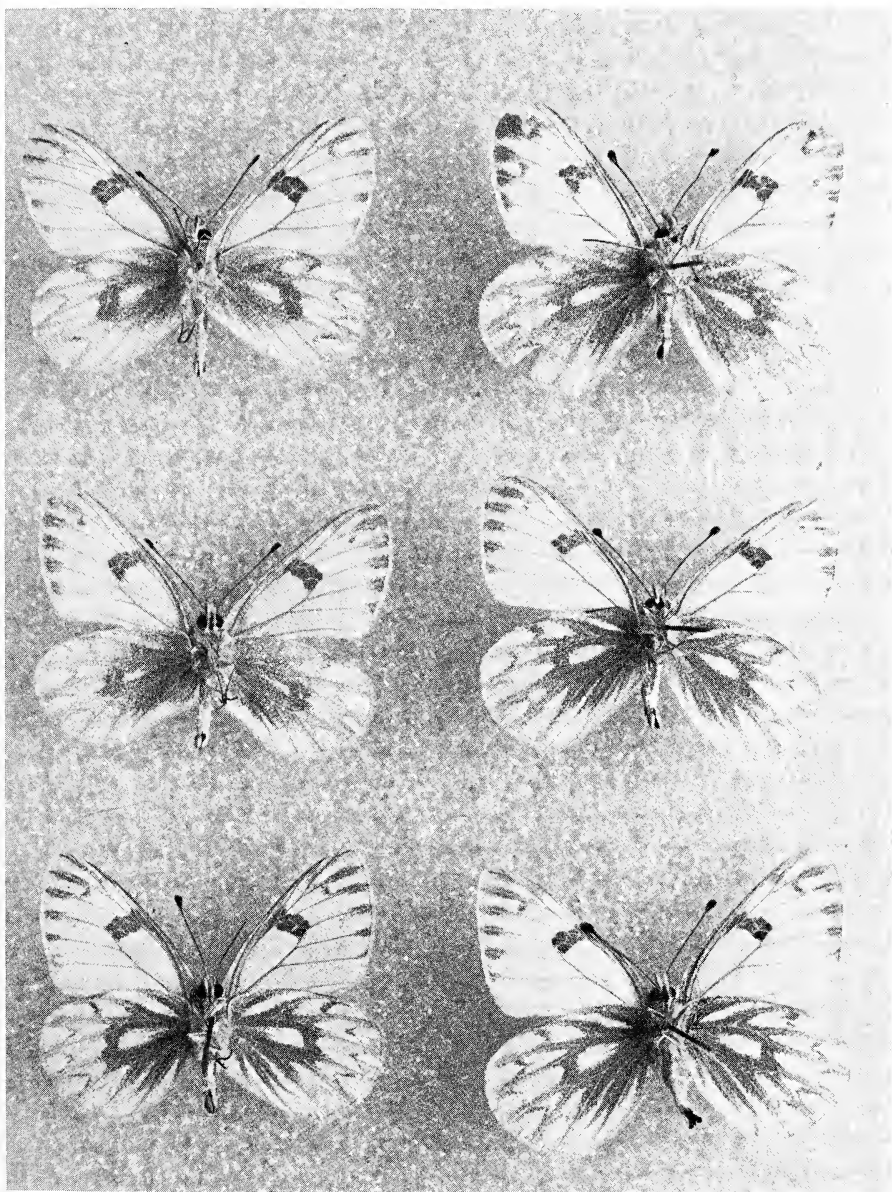


Fig. 5b.—Same but ventral.

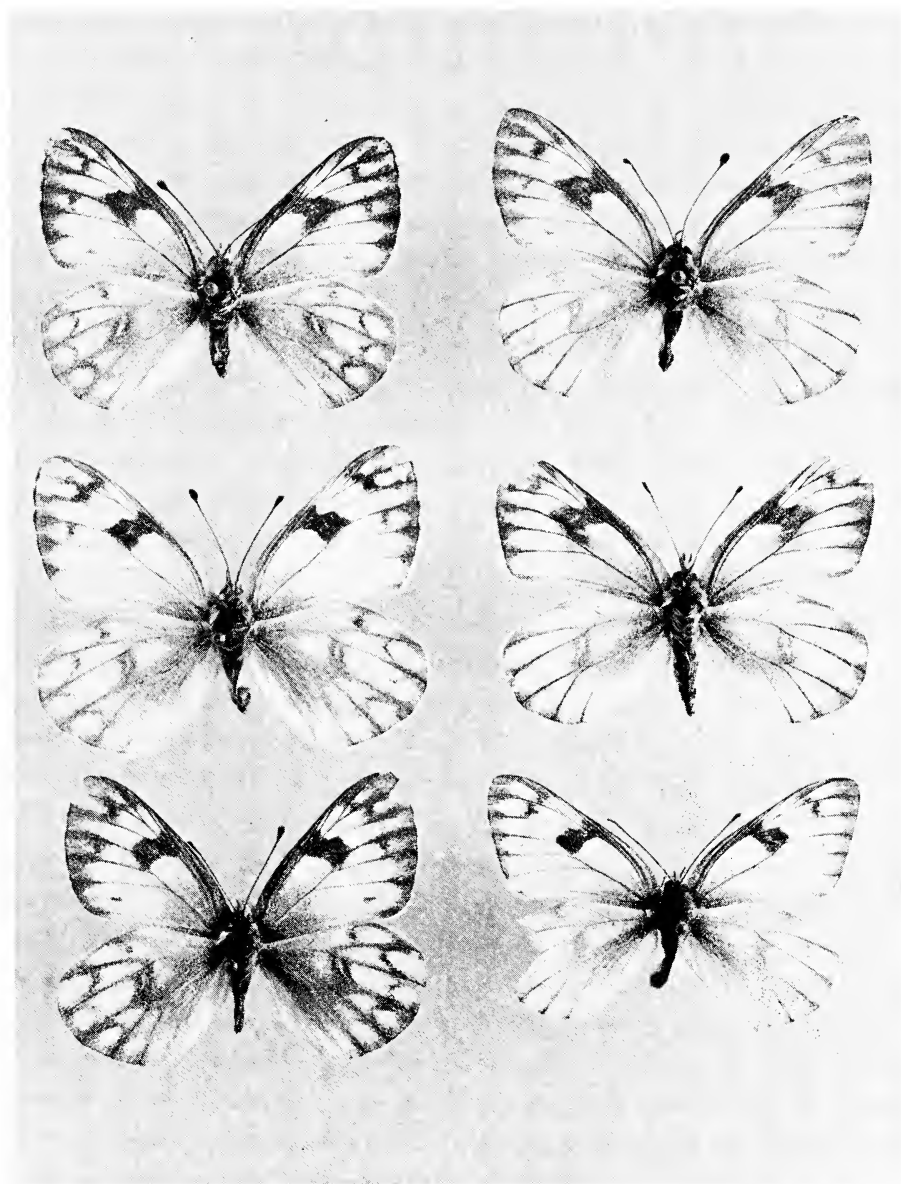


Fig. 6a.—Aberrant phenotypes of female *Pieris occidentalis neloni*, dorsal surfaces, illustrating light (estival) and dark (vernal) pattern.

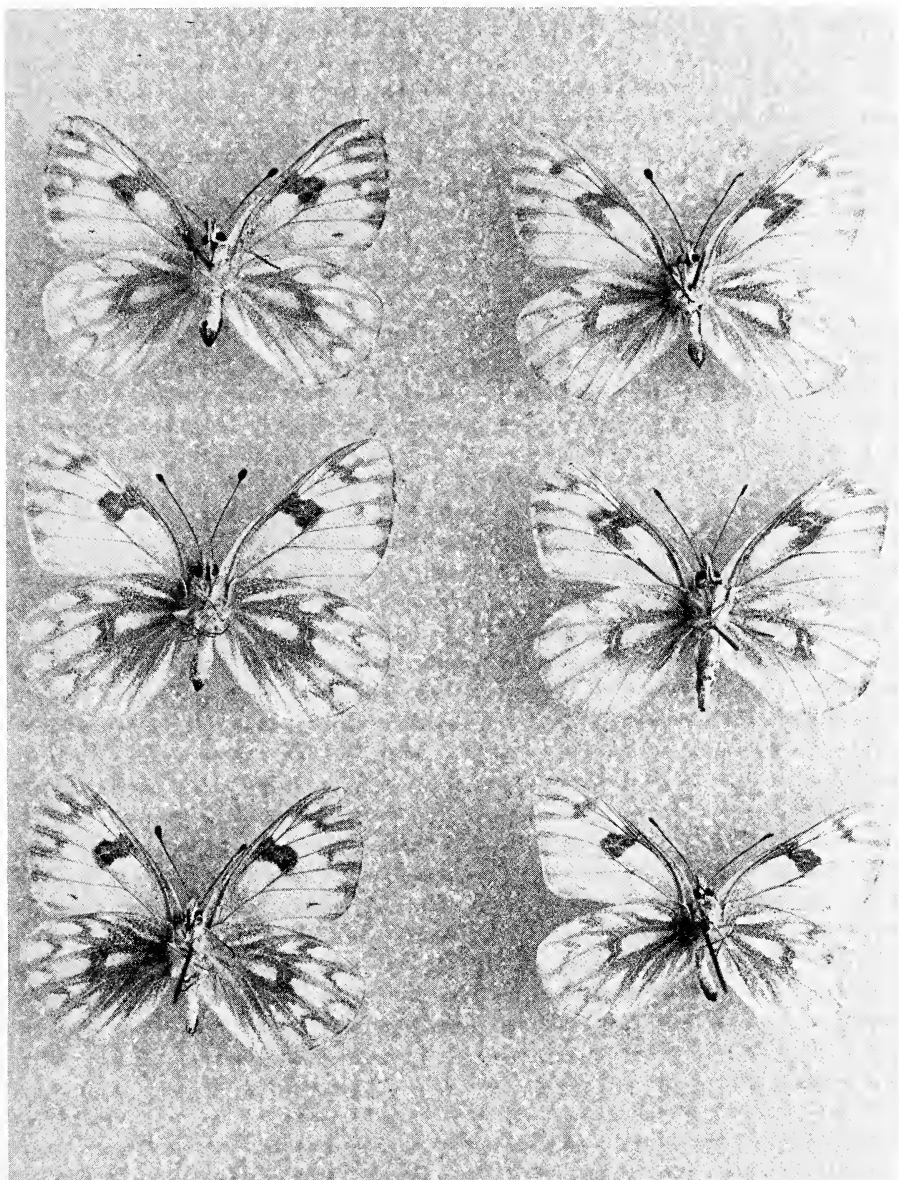


Fig. 6b.—Same but ventral.

the number of antennal segments. Some of these are illustrated in figures 7 and 8. These individuals were generally quite vigorous and lived 2-8 days, but most were unable to fly and all failed to mate, although the females were courted by normal males. These extreme phenotypes would presumably be lethal in Nature.

No wild specimens similar to those produced by this Fairbanks allele have been seen from any *Pieris occidentalis* population. Apparently, the male which mated with one of the founder females was heterozygous for it, but no examples were found among the 18 specimens collected at Fairbanks. The phenotype has some similarity to that of the mutant "ray" described from New York City stock of *P. protodice* by Shapiro (1973). The most extreme individuals produced in that line also somewhat resemble those reported here (fig. 9). However, "ray" is inherited as recessive. The dark "ray" along Cu on the forewing ventrally is perhaps produced in a variety of ways in this species group, as it occurs consistently (in females only) of Colorado *P. o. occidentalis* from above timberline and is inherited as a sex-limited dominant in crosses with Sierran stock (Shapiro, unpublished data).

Homozygous "ray" females often show stripping of scales along the outer margin below the forewing apices dorsally (Shapiro, 1973). This trait was observed in many Fairbanks specimens, both "wild type" and aberrant, and with equal frequency in both sexes. It may reflect adhesion of the wing to the pupal cuticle, such as occurs in the "albinensis" trait in *Pieris brassicae* Linnaeus (Gardiner, 1962). No difficulties with eclosion were observed in the pure Fairbanks line, but Gardiner was able to select for a line of *P. brassicae* in which "albinensis" eclosed normally, and the same selection may have occurred naturally at Fairbanks. When this trait was recombined with a California genome the system could have been disrupted, thereby contributing to the unusually high mortality of fully pigmented, ready-to-eclose pupae in the F₂. Only one adult which eclosed, the *nelsoni*-phenotype male, displays it.

The nature of the abnormalities observed in the Fairbanks material parallels those found in mass-reared stocks of *P. protodice* closely enough that one may assume similar developmental pathways are involved, whether or not the genetic control is homologous. Curiously, these abnormalities have not yet been seen in California *P. occidentalis*.

DISCUSSION

The hybridization experiments leave little doubt that *Pieris nelsoni* Edwards 1883 and *P. occidentalis* Reakirt 1866 are conspecific. By the International Code of Zoological Nomenclature, the former should be considered a subspecies of the latter, and written as *Pieris occidentalis nelsoni* (this combination was used by dos Passos, 1964). Left unresolved is the relation of both to *P. callidice* Hübner 1805, of the Palearctic region. This relationship can be clarified only by genetic experimentation.

The small size of the F_1 and F_2 Fairbanks x California broods precludes any convincing statistical analysis of the inheritance of phenotypic differences between the stocks, but it is evident that they must differ at several loci influencing color and pattern. In the case of differences in thresholds for diapause and phenotypic induction, these differences are clearly adaptive for the subarctic *nelsoni*. Even the aberrant phenotypes recovered from the Fairbanks stock would be potentially adaptive if the concentration of melanin at the hind wing base ventrally contributes to body warming during lateral basking. Strikingly, the reduction of the dorsal black pattern in the subarctic *nelsoni* parallels the appearance of extreme vernal phenotypes of *P. protodice* which fly in early spring in both eastern and western North America, suggesting an inherent advantage to this pigmentation under low-temperature conditions.

The hybrid broods are again too small for much to be said with confidence concerning the strength of postzygotic barriers, except that the fertility and viability of the F_2 did not depart significantly from many pure broods of both parental stocks when reared under high temperatures and continuous light. The sex ratio of the F_2 was normal. In butterfly hybrids involving genetic barriers there is usually a deficiency of females (the heterogametic sex). As noted previously, the high incidence of pupal mortality in the F_2 was not duplicated in the pure Fairbanks line but has been seen in some lots of Sierran pupae held at high temperatures in continuous culture; in these cases, however, most of the mortality occurs before adult pigment is laid down, while in the F_2 it was after.

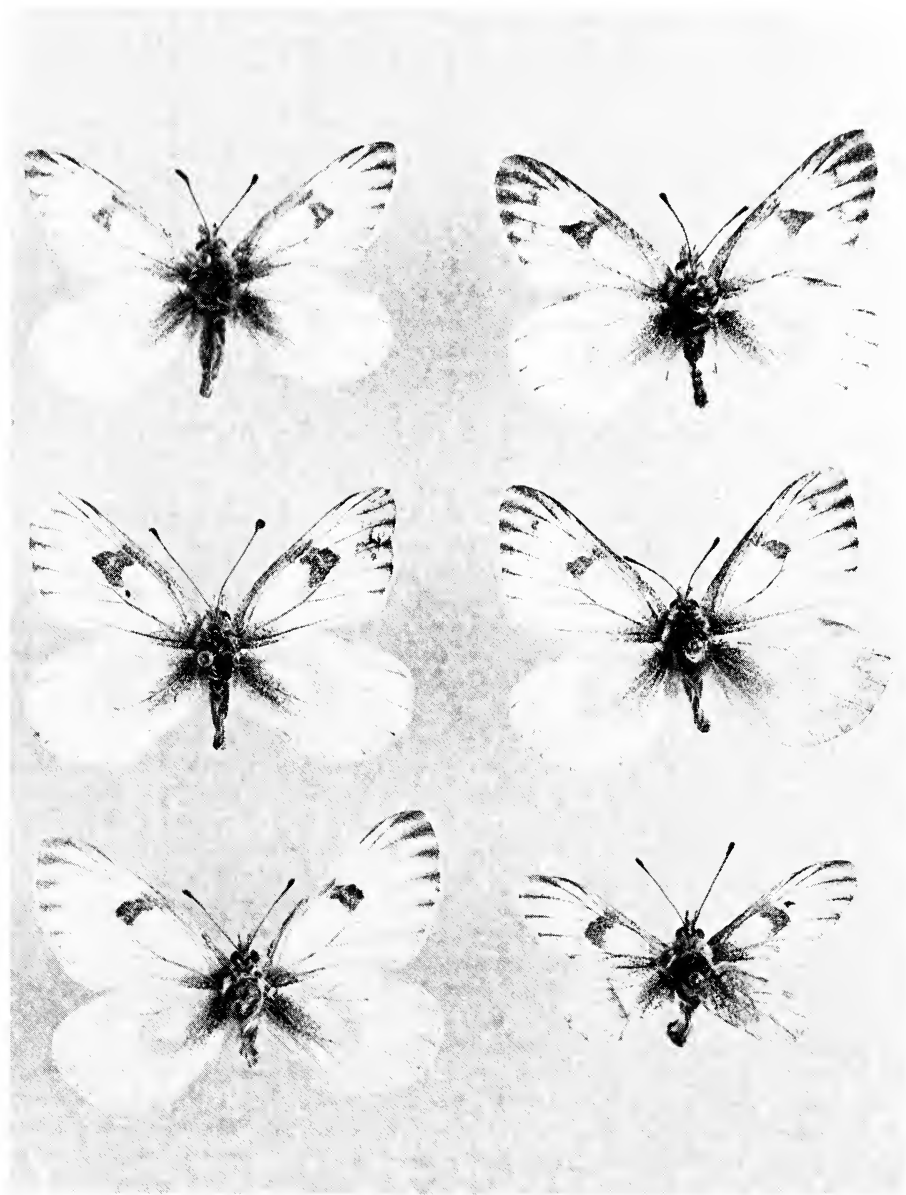


Fig. 7a.—Dorsal surfaces of extreme aberrant *Pieris occidentalis nelsoni* males.

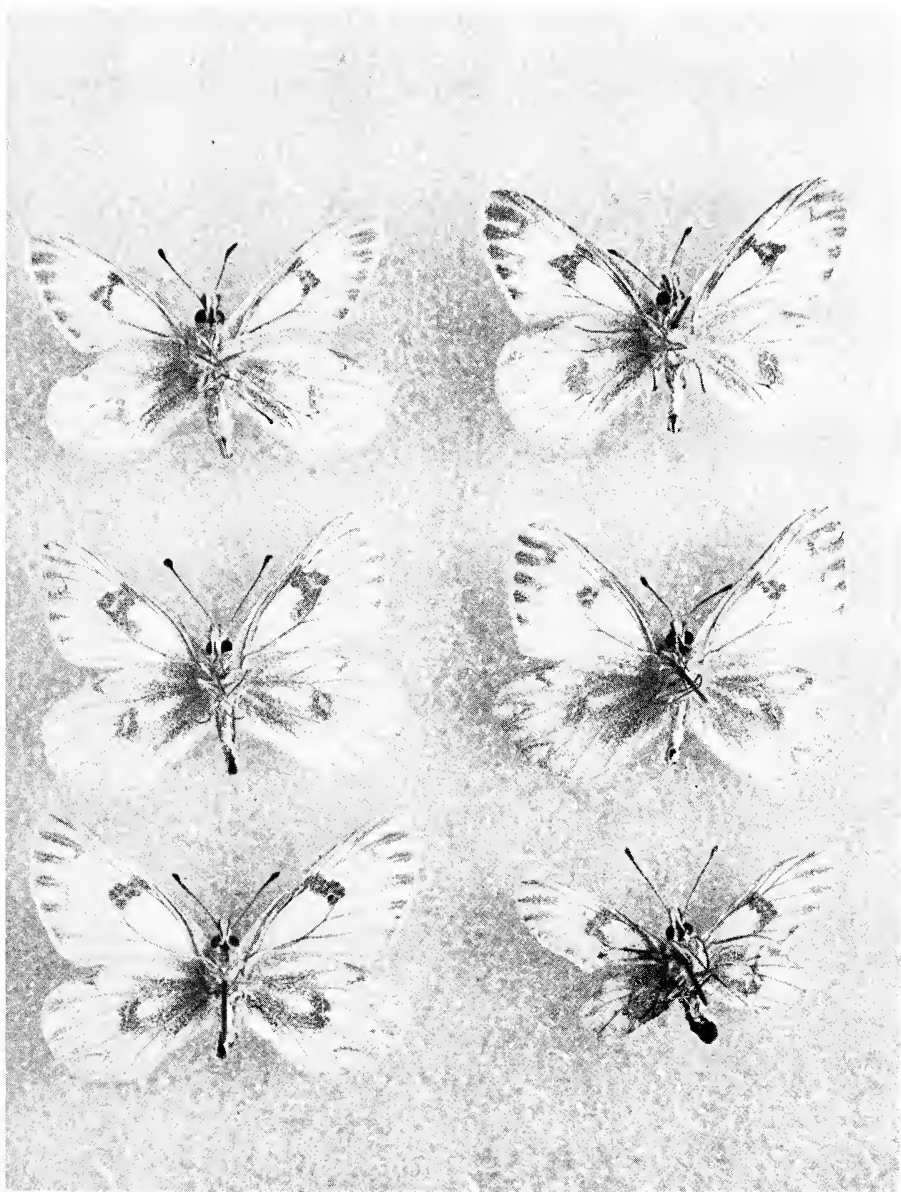


Fig. 7b.—Same but ventral.

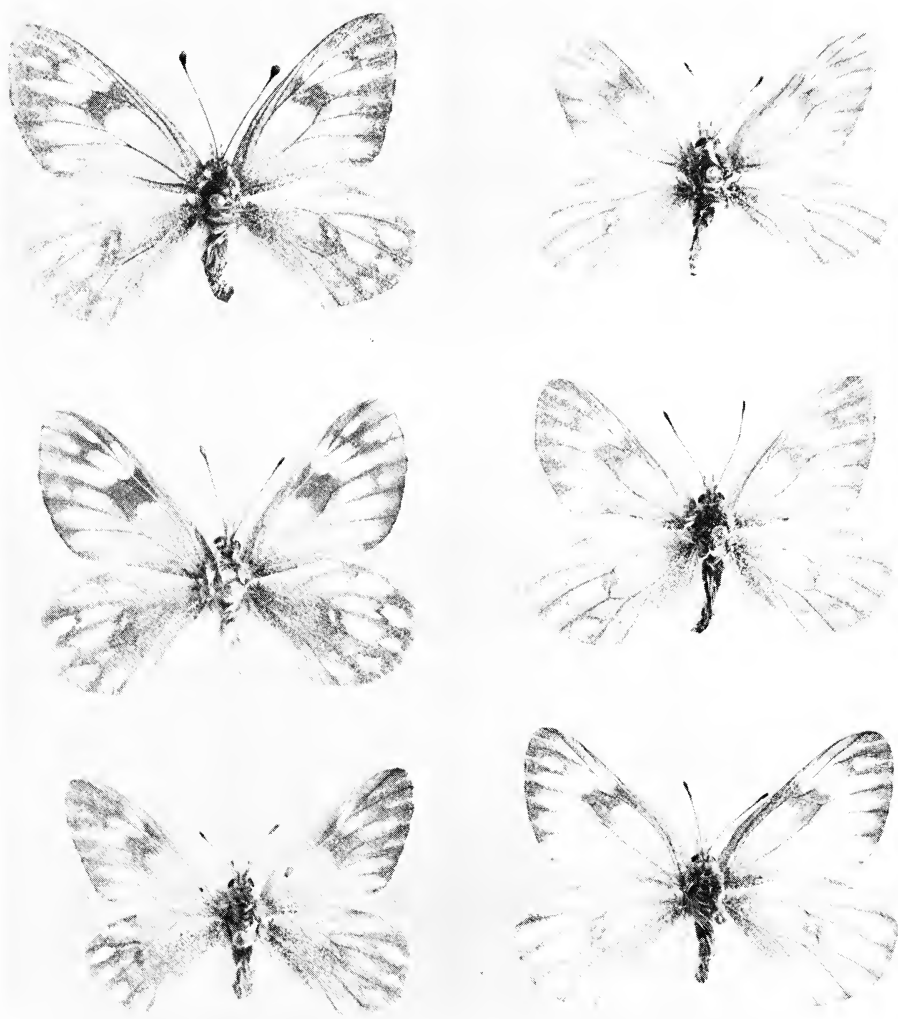


Fig. 8a.—Dorsal surfaces of extreme aberrant *Pieris occidentalis nelsoni* females.

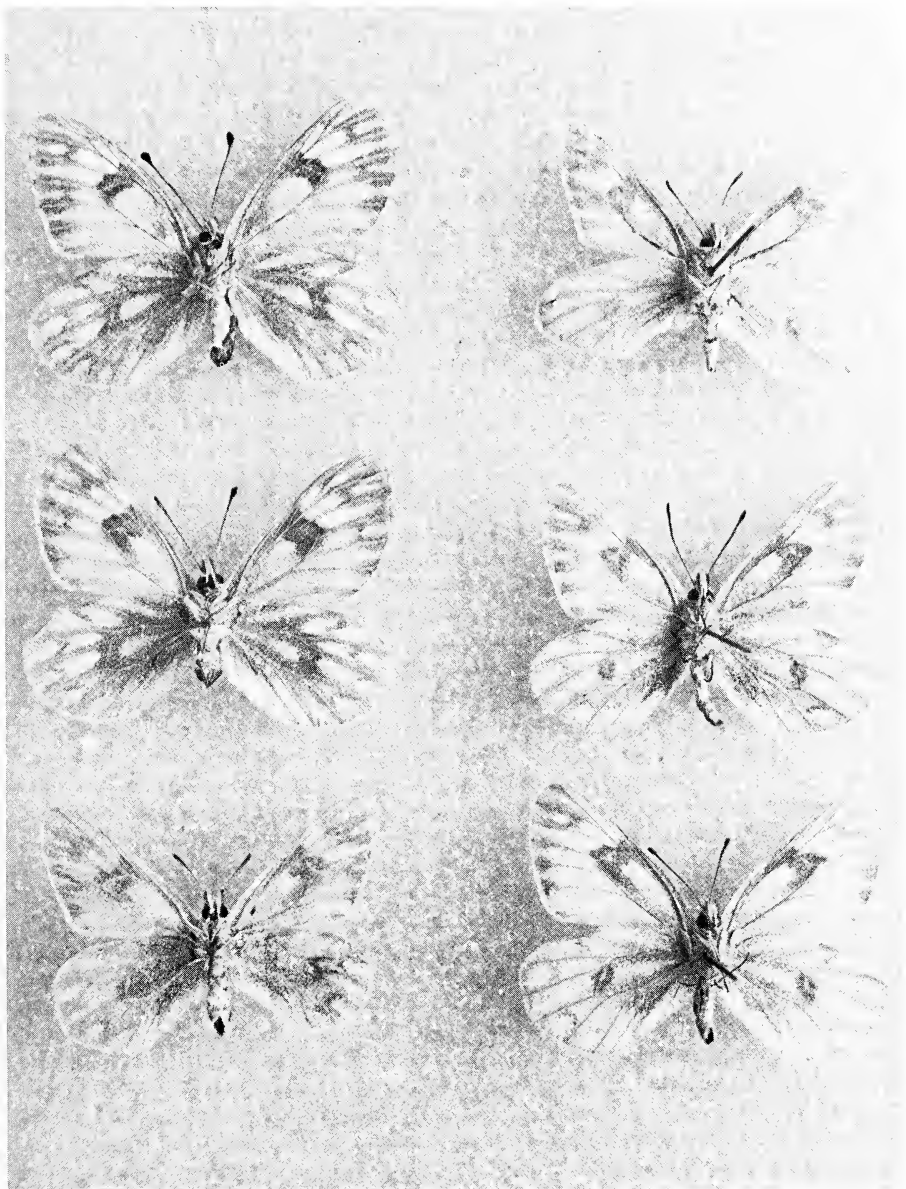


Fig. 8b.—Same but ventral.

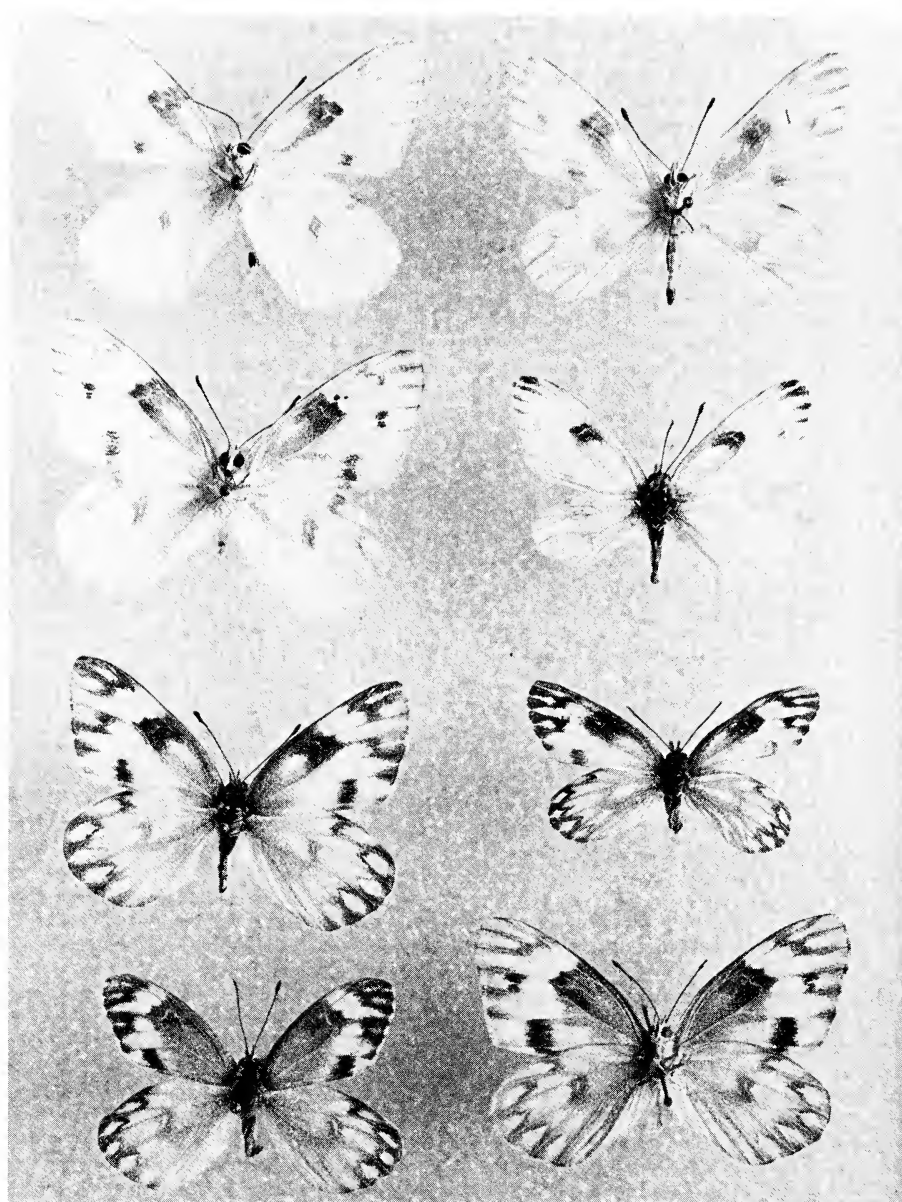


Fig. 9.—Selected examples of extremely aberrant *Pieris protodice* of the "Ray" line for comparison with Fairbanks stock of *P. o. nelsoni* (see Shapiro, 1973).

SUMMARY

1. Hybridization experiments demonstrate the apparent conspecificity of the taxa "*Pieris nelsoni*" from Alaska and *P. occidentalis* from the Sierra Nevada of California.
2. Three bred F_1 hybrids between these taxa were basically of the California phenotype, but within an F_2 of 25 individuals phenotypic variation was very great and recombination among several loci was evident.
3. An aberrant phenotype of *P. o. nelsoni* was obtained from the Fairbanks stock; it is inherited as an autosomal dominant. A few individuals exhibit functionally lethal exaggerations of the characteristics of this phenotype.
4. Aspects of the genetic variation of *P. o. nelsoni* are shown to parallel the related species *P. protodice*, which was studied previously.

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Mr. S. R. Sims assisted in field work in California and Mrs. A. R. Shapiro did so in Alaska.

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EARLY STAGES OF *PHYCIODES PALLIDA*, *P. ORSEIS*, AND *P. MYLITTA* (NYMPHALIDAE)

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Department of Entomology, University of California, Davis, California

SCOTT (1973) DESCRIBED EARLY STAGES of *P. orseis*, compared them with published descriptions of early stages of *P. mylitta*, and speculated that *P. orseis* might be most closely related to *P. pallida*.

This speculation has proven false. *P. pallida* from Red Rocks, Jefferson County, Colorado, was raised on *Cirsium vulgare*. *P. mylitta* from Thompson Canyon, Yolo Co. Calif. and near Copper, Siskiyou Co. California were raised on *Silybum marianum*. *P. pallida* differs in having later instar larvae ochre in color rather than maroon black as in *P. orseis* or light maroon brown as in *P. mylitta*. *P. pallida* mature larvae have a dorsal brown line, a brown band through the supraspiracular setae, and a few other brown spots. Mature larvae of all three species have the dorsal white stripe on the head. Mature larvae of *P. pallida* lack the subdorsal light spot on the head present in *P. orseis*, but have a light area just above the ocelli (absent in *P. orseis*). *P. mylitta* rarely have the subdorsal light spot and rarely have the supraocellar light patch.

I conclude that phenetically *P. orseis* and *P. mylitta* are most similar to each other, and *P. pallida* is more distantly related but is more similar to *P. mylitta* than to *P. orseis*.

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RECENT CAPTURES OF *ANTHOCHARIS CETHURA CATALINA* MEADOWS

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THE CATALINA ORANGE-TIP, *Anthocharis cethura catalina* (Pieridae), was described by Meadows (1936) from a series of eight males and four females, collected from 1928-1933 at various locations on Santa Catalina Island, California (Grand Canyon, White's Landing, Renton Mine area, Salta Verde, and Little Harbor). The holotype (from Grand Canyon) and allotype are currently in the Natural History Museum of Los Angeles County collection, and a series of paratypes (one male, two females) are in the University of California, Irvine Collection (Charles Rudkin collection). Other paratypes are housed in a portion of the Don Meadows collection, currently at the Bower's Museum (Santa Ana, California). Strangely enough, over forty years later, these twelve specimens were still the only known (or publicized) representatives of this subspecies. Some Lepidopterists had postulated that the subspecies may have become extinct in the intervening years since its description (Emmel and Emmel, 1973). In fact, at the time of this writing, the Office of Endangered Species (Washington, D. C.) was investigating the possibility of placing the Catalina Orange-tip on the Endangered Species List (Federal Register, 40(55):12691).

On a recent trip to the island, the author was able to verify the continued existence of *Anthocharis cethura catalina* and dispel any rumors to the contrary. Since almost nothing is known about the habits of this small desert butterfly which managed to attain an island foothold, it seems worthwhile to add my observations in the hopes that other Lepidopterists will be moved to initiate other studies on this local subspecies.

The author, accompanied by another collector (C. R. Roseland), visited the Avalon area on 20 April, 1975, collecting from 1100 to 1530 PST (daylight savings). Calm, warm (74° F.)

weather prevailed, the sun being obscured but briefly during this time by haze. Meadows (1936) had stated that "the most accessible locality where *catalina* may be collected is a small, open meadow at the top of a ridge between Renton Mine and Jewfish Point, two miles south of Avalon." Thus, it was decided to try to reach this locality.

We started a grueling cross-country hike up the steep hills south of Avalon, moving up a fire break at the top of the second ridge from the ocean. Not one butterfly was seen during the first hour of hiking. However, as the sun warmed the island, a few *Celastrina argiolus echo* (Lycaenidae) began to fly in the chaparral areas. The first Catalina Orange-tip (so we assumed) was sighted at time 1215, flying along the steep south-west slope of the ridge, at an elevation of 500 feet. The slope, covered with a rich carpet of grass and other annuals at this time of year, also had vigorous growths of California Sage (*Artemesia californica*), with some sumac (*Rhus laurina*) and *Opuntia* also present. The specimen which was sighted proved impossible to collect. We continued up the ridge via the firebreak until we reached an elevation of approximately 650 feet. It was then that I saw the first Avalon Hairstreak of the day (*Strymon avalona*). At the same time, however, we sighted two orange-tips flying up the northeast slope and over the ridge. Neglecting *avalona*, we managed to capture both butterflies in flight, and a glance at the ventral wing pattern left no doubt that we had just captured *cethura catalina*! The specimens captured turned out to be two males. We continued up the ridge to an elevation of about 1100 feet without additional captures of the Catalina Orange-tip, although we observed or captured a few *avalona* flying about the long-dead blossoms of *Rhus laurina*, one Orange-tip, *Anthocharis sara gunderi* (another island endemic), two *Papilio zelicaon*, and 2-3 additional orange-tips that may have been *catalina*. When the ridge twisted, facing South, we followed, sighting perhaps 2-4 *Anthocharis*, although none could be captured, due to their swift and erratic flight over the rough terrain.

As we started hiking in the southern direction, down a ridge adjacent to the southwest of the one on which we had captured our first *catalina* (a course leading back to Avalon, as we no longer had time to pursue our hike to the Meadows locality near Renton Mine), we began to see considerably more *Anthocharis*. This ridge was covered with dense impenetrable chaparral flora,

broken only occasionally by grassy areas. The majority of the orange-tips captured, however, were *A. sara gunderi*. However, at an elevation of 1100 feet (time approximately 1445), a male and female *catalina* were seen flying up the slope and were captured. The female was somewhat aberrant in that the normal dorsal orange marking was considerably reduced, being retained only along the veins in the subapical area, giving a somewhat streaked appearance. Both specimens were in fresh condition.

The remainder of the trip proved uneventful.

Several statements can be given concerning the habits and status of *cethura catalina*, even though our excursion to *catalina*'s habitat was brief. First and foremost, the Catalina Orange-tip is still extant on Santa Catalina Island. Additionally, fear that the subspecies was presently endangered appears unfounded. The butterfly was found on two ridges, half a mile apart, adding to the already know extensive, although spotty distribution of the subspecies on the island (see Figure 1). The Catalina Orange-tip may probably be expected to occur on many, if not most, of the rather inaccessible ridges in the area near Avalon. We should note that the butterfly has managed for years to survive the onslaught of the environment by goats (introduced by the Spanish hundreds of years ago) and wild boars, and it is doubtful that the butterfly will succumb to any analogous habitat changes (grazing, recreational use). Indeed, the butterflies seemingly were not affected at all by the defoliated firebreak up the first ridge, and were sighted more often on this ridge than on the more natural appearing adjacent ridge. Further observations on the populations, however, are required before the true status of the subspecies can be determined. Commercial development is not being planned for any *catalina* habitats, most of the island now being a preserve, and thus the butterfly is probably in no danger for many years to come.

No strong hilltopping behavior was observed. Perhaps as many individuals were seen fifty or more feet down the slopes of the ridges as were seen anywhere near the top, hence why so few specimens could be procured. The erratic flight typical of *cethura*, however, was observed in *catalina*.

The date of our captures is of interest, particularly in regard to the freshness of specimens. Meadows (1936) captured *catalina* from March 23 to April 9, his last capture being almost two weeks previous to ours. The flight period given by Emmel and Emmel (1973) and Meadows (1936) should thus probably be

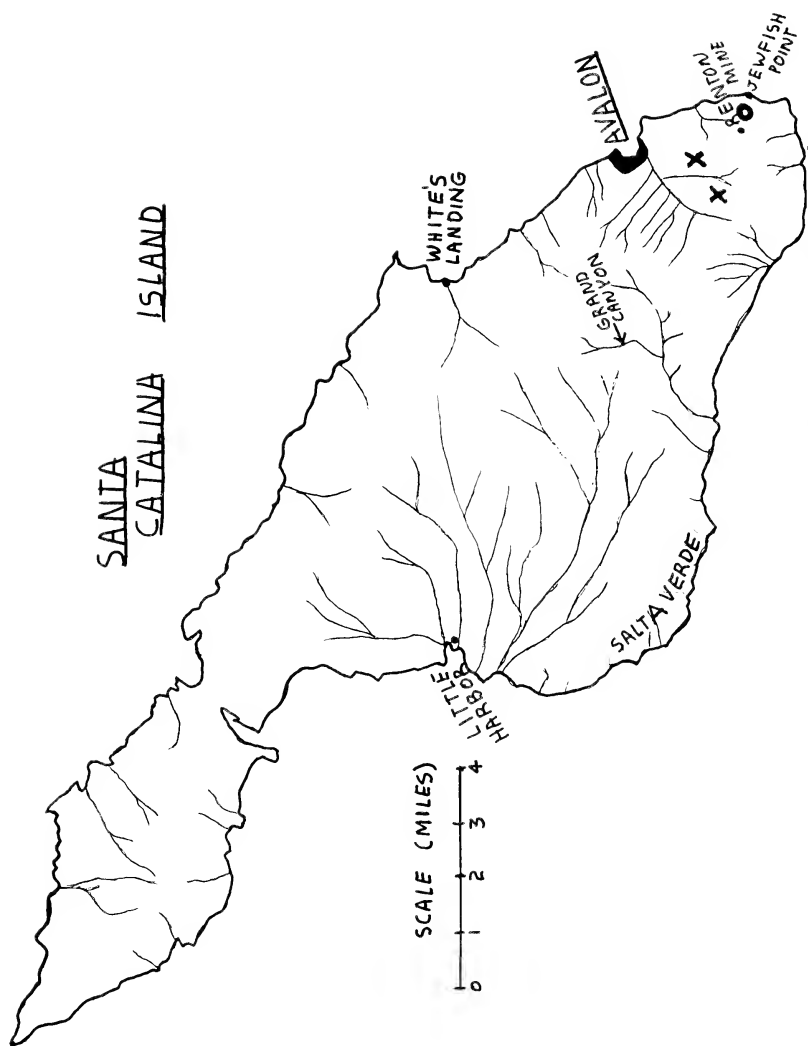


Fig. 1.—Santa Catalina Island, California, indicating localities where *Anthocharis cethura catalina* has been captured. (X) designates recent capture localities by the author, (O) designates Meadows' collection localities. Specific localities at Little Harbor, Salta Verde, Grand Canyon, and White's Landing are not given in Meadows (1936) or on labels accompanying specimens in the type series.

amended to read "late March to late April". Late Spring rains in 1975, however, could have caused an unusual delay in the adult emergence of *catalina*, as such delays were reported for many southern California butterflies during this season.

It is rather surprising that captures of the Catalina Orange-tip have not been reported in so many years, although numerous Lepidopterists have visited Santa Catalina Island in order to procure specimens of the other two endemic butterflies found on the island. This may be attributed to the past and present inaccessibility of *catalina* habitats (physical and/or legal), short flight period of adults, possible confusion with *Anthocharis sara gunderi*, and the tendency of local collectors not to exert much effort searching for a relatively unspectacular-appearing butterfly (versus the amount of effort expended to find the legendary lost Atossa Fritillary, *Speyeria adiaspe atossa*, of southern California).

I would like to acknowledge the help of Mr. Craig Roseland in securing specimens, Mr. John Haynie, our pilot to the island, and the Xerces Society, which has provided financial and moral support for studies in rare and endangered southern California Rhopalocera. A voucher specimen of *cethura catalina* from this trip will be deposited in the collection of the Natural History Museum of Los Angeles County.

AUTHOR'S NOTE: Three additional records of the Catalina Orange-tip came to light as a result of the distribution of preliminary drafts of the above article, but were received after the article went to press. Dr. Charles Remington informs me of the existence of two specimens collected by Charles Ingham and purchased through the Ingham collection, now housed at Yale University. The only *recent* record to come to light in addition to my collecting experiences is that of Dr. Jerry Powell of the University of California, Berkeley, and Dr. Paul Opler (presently of the Office of Endangered Species, Washington, D.C.). On April 1, 1968, a specimen of *catalina* was taken by them at Little Harbor during a lull in generally bad weather. This fairly recent capture indicates the continued existence of *catalina* from more than one locality on Santa Catalina Island.

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OLD TIMERS
JOHN ADAMS COMSTOCK
ENRICO PIAZZA

ONE OF THE FIRST ENGLISH lepidopterists that I met here in Southern California was Enrico Piazza. He was collecting for Rothschild of the British Museum.

His actual name was Henry Place, but he went to Italy early, was a grand opera singer, and italianized his name for professional reasons. When his voice gave out, he commercialized his hobby, and came to Southern California. I visited him in a cottage which he had rented in San Diego, and admired the fine condition of the moths he was preparing for his customers.

Four species of California moths were named for him, namely:

Tornos piazzata Cassino & Swett.

Cosymbia piazzaria W. S. Wright

Raphia piazzii Hill.

Myelois piazzella Dyar.

He became ill, and started for England, but died in New York of cancer. Nothing was known of his effects, and his key collection was lost. His types had probably been sent to England.

I have not been able to locate essential facts concerning his background.

FORDYCE GRINNELL JR.

Fordyce was our most prominent and active lepidopterist when I arrived in Southern California. He was living in Pasadena with his parents. He was born June 17, 1882, in Pine Ridge, South Dakota, son of Dr. Fordyce Grinnell Jr. and Elizabeth Pratt Grinnell.

His brother was Joseph Grinnell Ph.D., a noted ornithologist and Faculty member of the University of California.

Fordyce was the founder of the Lorquin Natural History Society (now the Lorquin Entomological Society.) He was very active in collecting lepidoptera and had many local neophytes whose leadership he followed from about 1900 to 1914, when he entered Stanford University.

Read by John A. Comstock at the Association Banquet, evening of June 19, 1965.

He obtained his Bachelor degree in 1918, and went to Hawaii in the same year. He taught there until 1921 when he returned to Stanford.

Then, in 1922 he went to the Philippines where he served under the Bureau of Education of the Philippines, as a teacher.

He resigned in five months because, in his own words "he was unsuited to the official red tape and the classroom grind."

Thereafter he collected butterflies and beetles for the Bureau of Science in Manila, and the Hill Museum in Surry, England. This took him through various portions of the Philippine Islands until March of 1923, when he sailed for Australia.

He collected specimens in widely separated parts of the continent, interspersed with odd jobs to replenish his funds, until 1930, when he arrived in Cooktown, Australia. There he received a letter from his mother asking him to return home.

Mrs. Grinnell was then living in Sausalito, a widow, 80 years of age. Fordyce lived with her until he married Mary D. Walters on August 10, 1937. The ceremony occurred in Muir Woods.

I have no further record of his activities until he died in San Francisco, July 20, 1943.

He was author of the following species of butterflies:

Anthocaris lanceolata australis. *Cercyonis behrii*. *Vanessa atalanta* ab. *edwardsi*. *Vanessa carye* ab. *intermedia*. *Vanessa carye* ad. *letcheri*. *Strymon sylvinus desertorum*. *Plebejus emigdionis*. *Glaucopsyche lygdamus australis*. *Erynnis persius pernigra*. *Erynnis callidus* ♂ (nec. ♀) (syn. *lacustra callidus* ♀ partim) *Polites sabuleti tecumseh*.

WILLIAM SHERMAN WRIGHT

William S. Wright was an early staff member of our own San Diego Museum of Natural History. He served as Curator of Insects from 1922 to 1933, in addition to holding the important post of County Supervisor of Nature Study. He was a specialist in the *Geometridae*, and his own collection of insects, with his types, served as the nucleus of our present Entomological Division.

He was a profound student, a capable administrator, and a beloved teacher and friend.

A bronze plaque commemorating his generosity and helpfulness to our Museum may now be seen in the Entomological Laboratory.

He was born in Plaino, Illinois, April 23, 1866, and died in Laguna Beach, California, July 8, 1933.

I knew him well, and frequently collected with him, but, regretfully failed to make notes of the background of his history and family. There is little that I can find in the biographies.

He published several new species, and a number were named for him, but I have not had time to list them.

WILLIAM GREENWOOD WRIGHT

Most of us have heard of the colorful pioneer lepidopterist of our early Southwest, but very few have seen his monument in the shape of his volume on "THE BUTTERFLIES OF THE WEST COAST".

The tragic reason is that "at the great fire in San Francisco, April 18, 1906, all the items going to make up this book . . . consisting of everything in the printers and the binders hands, and the finished books . . . all were destroyed."

I have one of these books, thanks to the fact that Wright's possession were given to the California Academy of Sciences in San Francisco, including the few books that were in San Bernardino when the fire occurred. I was able to buy one of these volumes, and you can now take a peek at it.

W. G. Wright was born in 1830, and died in 1912. There may have been memorial notices of him, but I have failed to find only the one by Fordyce Grinnell in the Entomological News, Vol. 24, pp. 91-92, 1913. My notes contain mainly hearsay from people who knew him. He was a planing mill owner, whose hobby was butterfly collecting, and had had very little formal schooling. His book evidences that fact, but it also shows that he had enthusiasm and purpose. Knowing his handicaps, I consider that he did a remarkable piece of work.

There are many errors, to be sure, but others have pointed these out, as, for instance, Henry Skinner and Fordyce Grinnell in the Entomological News in Vol. 16, pp. 336-340, 1905.

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WHY DO CALIFORNIA TORTOISESHELLS MIGRATE? ¹

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THE CALIFORNIA TORTOISESHELL BUTTERFLY, *Nymphalis californica* Boisduval (Nymphalidae), is well known to entomologists and laymen alike on the Pacific Coast for its mass movements. The biological basis for these movements has always been obscure. After discussing notable outbreaks in the Yosemite region, Garth and Tilden (1963) say: "The explanation seems to be that the California Tortoiseshell is a swarming species which, like the lemming, has cycles of abundance followed by a drastic reduction in the population . . ." But this is obviously no *explanation* at all. Powell (1972) wrote that "the records suggest that this species periodically develops an imbalance with factors in its population equilibrium at isolated sites, followed by mass emigration of adults in various directions. . . . *Nymphalis californica* should not be considered a migratory species except in the broadest sense." This is a more definitive statement, but it also falls short of being an explanation. Mass movements of butterflies, as Klots (1951) observes, have been attributed to "population pressure" and "parasite pressure." Just what do such "explanations" mean?

Let us assume that the word "migration" is applicable to *N. californica* as I intend to show it is. If we ask "Why do California Tortoiseshells migrate?" we are not asking a simple question. Ernst Mayr (1961) pointed out in a classic paper that any "why" question in biology may be answered at several levels. Mayr actually addressed himself to a question about migration: "Why did the warbler on my summer place in New Hampshire start his southward migration on the night of the 25th of August?" Mayr perceived at least four equally legitimate levels of causality:

1) *an ecological cause*. "The warbler, being an insect eater, must migrate, because it would starve to death if it should try to winter in New Hampshire."

¹Address prepared as invitational research lecture, 1975 Summer Advising Conference, UC Davis.

2) a *genetic cause*. "The warbler has acquired a genetic constitution in the course of (its) evolutionary history which induces it to respond appropriately to the proper stimuli from the environment."

3) an *intrinsic physiological cause*. "The warbler . . . responds to the decrease in day length and is ready to migrate as soon as the number of hours of daylight has dropped below a certain level."

4) an *extrinsic physiological cause*. ". . . sudden drop in temperature and associated weather conditions affected the bird, already in a general physiological readiness for migration, so that it actually took off on that particular day."

Mayr groups (3) and (4) as *proximate* causes of migration—the immediate triggering mechanisms. Causes (1) and (2) he calls *ultimate* causes—"causes that have a history and that have been incorporated into the system through many thousands of generations of natural selection." Clearly a physiologist, asked our "why" question, would refer to proximate causes; an evolutionist, to ultimate ones. Equally clearly, cause (1) is the basis for the natural selection which brought (2) into being, and (3) is the phenotypic manifestation of the genetic information in (2), and is brought into action by (4). This method of causal analysis is theoretically applicable to any adaptation; and by its use we may perhaps be spared the travail of endless controversies over the significance of a phenomenon such as hilltopping behavior in butterflies and other insects, or of "territoriality" in anything. Let us now try to analyze levels of causality in the light of what we know of *Nymphalis californica* migrations—which is not much, but is considerably more than many people think we know.

I have been watching Tortoiseshell migrations for the past four years, and unlike most Tortoiseshell watchers, I have been chasing them. When you follow their movements from place to place—not by individual marking, which would truly be a needle-in-the-haystack operation, but by keeping track of where the front of the migration is on consecutive occasions—it becomes clear that, at least at the latitude of Sacramento, Powell is dead wrong: Tortoiseshells do not go in all directions; they have a set seasonal directionality, with a spring-fall reversal. The confusion in many published reports is based at least in part on the "static observer" effect and on local eddies in the migratory flow produced by topography. But California Tortoiseshells go

north and east in May and June and south and west in September and October. The generalized pattern is for dispersal out of the central Coast Ranges in spring—northward in the higher ranges, especially from Colusa County north, eastward from the lower ranges in Napa, Yolo, and Solano Counties, crossing the floor of the Sacramento Valley and going up the Sierra foothills east of Sacramento. Almost simultaneously Tortoiseshells migrate out of the Sierra foothills, heading upslope in a N to NE direction. The two currents generally merge. The pattern is exactly reversed in the fall; again the migrants can be seen crossing the Valley floor, where they never breed (there being no hosts). This pattern, first described in my 1974 paper based on 1972 observations, has been repeated unerringly in successive years; and as I get more sophisticated at Tortoiseshell-watching, I am getting better too at predicting the dates. They are rather variable; for example, the eastward-moving spring front passed through Davis on 26 May 1972, 9 June 1973, 6 June 1974, and 13 June 1975. Based on this small sample, the warmer and drier the spring, the earlier the flight. These migrants are, of course, not the adults which crossed the Valley the autumn before and overwintered (very few Tortoiseshells seem to remain in the lower Coast Ranges through the summer, and the hibernators are mostly or all immigrants from the north or east). They are their offspring. And the return migrants in fall are *their* offspring, or even their grandchildren.

The regularity of this pattern suggests that it is an adaptation, an attribute of the animal which promotes its welfare. Being an evolutionist, I am most interested in the ultimate levels of causality—the basis of natural selection resulting in the acquisition of a genetic program which instructs the animal to migrate in such and such a direction given such and such (proximate causality) conditions.

Why should *Nymphalis californica* leave the lowlands in both the Coast Ranges (which are often only foothills without any mountains) and the Sierras? Of course, it could be heat-intolerant. After all, its host plants, wild lilacs (*Ceanothus* species, Rhamnaceae), are green all summer; presumably it could breed continuously in the lowlands if it "wanted" to. Instead it leaves the foothills, with their *Ceanothus* species, to go breed in the high country and the north, with a different set of *Ceanothus*. It could be heat intolerance, acting directly; but I think not. Being a Pierid specialist, with a dislike for

Nymphalids as experimental animals, I do not want to test the following hypothesis myself. It would make someone a nice Ph.D. thesis, as well as being a good exercise in Mayr-style causal analysis.

In 1970, P. P. Feeny, from Cornell, published a landmark study of the role of host-plant chemistry in insect phenology. Feeny found that the spring feeding season of Winter Moth (*Operophtera brumata* L., Geometridae) larvae coincided with the period of minimal tannin concentration in their food—oak leaves—and that the higher tannin concentrations characteristic of mature, summer oak foliage interfered with nitrogen availability and perhaps leaf palatability to the larvae. Feeny was thus able to develop a causal explanation of spring feeding by Winter Moth larvae as an adaptive response to the seasonal pattern of nutritional “availability” of oak foliage. The insect faunas of high-tannin plants throughout the Northern Hemisphere appear to show this effect. Shapiro (1975) gives a schematic representation for some oak-feeding Lepidoptera in New Jersey, for example. Similar schemata could be prepared easily for Californian faunas on native oaks or on other high-tannin plants, such as *Cercocarpus*—or *Ceanothus*.

I am suggesting that California Tortoiseshells leave the lowlands and go upslope in spring because the lowland *Ceanothus* put on all their new growth in late winter-early spring and become nutritionally unsuitable for breeding by June. The higher one goes, the later the *Ceanothus* commence active growth and hence the later they have young, tender, hypothetically low-tannin foliage available for Tortoiseshell larvae. The seasonality of lowland *Ceanothus* of course reflects the arid-summer climate, so indirectly at least climate may be a “cause” of Tortoiseshell migrations. But, in Mayr’s sense, the ultimate cause—the ecological cause—would be the correlation of geography and availability of *Ceanothus* foliage. In California’s progressively drier Quaternary summer climate, a *Ceanothus* feeder unable to handle tannins has a “choice” between being sedentary and univoltine or migratory and multivoltine; I propose that *N. californica* has evolved along the latter course.

Sometimes the proximate and ultimate causes coincide, in whole or in part. The proximate causes of Tortoiseshell migrations could involve a response to the chemical or textural condition of the plants. They could also be tied to photoperiod, temperature, or some other seasonal indicator—we know not

what. At present, however, there is nothing to suggest that either population density or "parasite pressure" has anything to do with it. Based on my four years of careful observation, I am willing to assert that migration occurs in the directions described with population densities fluctuating by at least two orders of magnitude. If the host-availability hypothesis holds up, this would scarcely be surprising; inedible plants are inedible whether there are a few or a lot of hungry caterpillars.

In recent years major strides have been made in the understanding of insect migration, e.g. the sophisticated studies by Dingle (1968, 1972) and his colleagues on milkweed bugs (Hemiptera, Lygaeidae) in North America. There is no reason why butterflies should be any more difficult to unravel, especially once we realize that explanations at different levels are not mutually exclusive (but, rather, mutually complementary), and that naming a phenomenon ("swarming species," "cycles of abundance") is not the same as explaining it.

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EARLY WORK ON THE MEGATHYMIDAE

JOHN ADAMS COMSTOCK

My interest in Lepidoptera began in 1894, at 11 years of age, when living in Evanston, Illinois. This was appreciably stimulated by correspondence with a young collector living in Pasadena, California, named Fordyce Grinnell, whose address I found in the Entomological News. This contact cherished my hope that I would someday collect butterflies in California.

At that time I knew nothing of the 'giant skippers' called *Megathymidae*, since they did not occur in Illinois.

It was not until about 1920 that interest in the *Yucca* and *Agave* borers was aroused by a chance acquaintance with Commander Charles M. Dammers of Riverside.

Dammers brought his son Carlito to the Southwest Museum, where I was then Director, and asked my assistance in teaching the boy how to rear and illustrate the life histories of butterflies. This led to the father's interest in excess of the boy's capabilities, and resulted in Dammers cooperating with us in joint publication of numerous articles on the biology of California lepidoptera.

In 1932 we were able to successfully rear *Agathymus stephensi* (Skinner) on *Agave deserti* Engelman, and to publish its life history in Volume 33, (2): pages 81-86, 1934, Bulletin, So. Calif. Academy of Sciences.

This led us to an intensive effort to locate larvae of a *Megathymus*, the imago of which had been netted occasionally in association with Joshua trees — *Yucca brevifolia* Engelman, on the Mojave Desert. Commander Dammers and Carlito began a search on the Joshuas one forenoon, but Carlito soon tired, and stretched full length on the desert floor while Dammers climbed assiduously. Suddenly Carlito noticed a female *Megathymus* alighting on a baby *Yucca* plant of about 8 inches in height, which proceeded to lay an egg. A shout brought the Commander to earth. Sure enough, an egg, and by further searching, more on other young shoots. The problem was solved. The *Megathymus* larvae were root-feeders underground, never on or in the leaves.

It then became easy to locate the 'cones' on top of infested young plants, and dig down to the roots where the larvae were feeding in late winter, or the pupae resting below the cones in early spring.

The life history was published and illustrated in the same issue of the Bulletin as was that of *stephensi*. It was listed as *Megathymus yuccae navajo*, the name that had been given to me by Dr. Henry Skinner on a specimen sent to him for determination. Later (1956) the subspecies was named by Stallings and Turner, in the Academy "Bulletin" as *martini*, in recognition of Lloyd's fine work on the *Lepidoptera*.

Those of you who have worked on the *Megathymidae* recall that our San Diego Museum Curator of Insects, Charles F. Harbison, has described two species of *Agathymus* from Baja California, namely *comstocki* and *dawsoni*, and that I have described and illustrated the early stages of these. In addition, I have similarly treated *Megathymus evansi*. The main reason that I mention it is that, by comparison with the great amount of research made by such experts as Don B. Stallings, J. R. Turner, H. Avery Freeman, Dr. C. J. Remington and Dr. Ernest R. Tinkham, I fully realize the shortcomings of my own efforts.

With a complex group such as this, studies require methods of oviposition, careful association of larvae with specific food plants, exact location in the leaves or roots of the plants, sap or plant fiber feeding, setu and method of frass disposal, nature and placement of the frass, method of silk-lining of the tunnels, chromosome counts, and many other details.

This means that one must live in close contact with a given species if they hope to obtain an intimate picture of life activities. This is an exacting task.

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SUPPLEMENTARY RECORDS OF
BUTTERFLIES IN THE
SACRAMENTO VALLEY AND SUISUN MARSH,
LOWLAND CENTRAL CALIFORNIA

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SACRAMENTO VALLEY

THE FOLLOWING RECORDS ARE ADDITIONS to Shapiro, 1975a. New species are starred.

Chlosyne lacinia crocale Edwards. — This apparent introduction, which was fairly common in 1973 at one locality (Camp Pollock, Sacramento County), was not seen in 1974. The habitat was flooded during much of the winter of 1973-74; it lies in the American River By-Pass.

**Nymphalis milberti* Latreille. — A single worn female taken iv.6.74 in North Sacramento, elevation circa 15 feet, in a colony of the introduced European nettle *Urtica urens* L. Presumably immigrant from higher elevations (Shapiro, 1975b).

Polygonia satyrus Edwards. — A second Davis record, female, vi.14.74. Since there are no nettles anywhere near Davis, the occurrence of this species there must be based on rare strays unless it breeds on the introduced Urticaceous ground cover *Soleiroleia* as does *Vanessa atalanta* L., which however is common.

Limenitis bredowii californica Butler. — There is still no evidence of breeding on the Valley floor, but an unusual number of observations of adults were made in 1974. At Davis seen v.25, ix.1, x.27.

**Callophrys dumetorum* Boisduval. — The first Valley record, fresh male, Beach Lake, Sacramento County, iii.21.74. Presumably breeding, but host not determined.

Pieris sisymbrii Boisduval. — Second Valley record: female, Southport, Yolo Co., iv.14.74. Presumably a stray from the foothills.

**Euchloe hyantis* Edwards. — A single male taken among the very common *E. ausonides*, Beach Lake, Sacramento Co., iii.21.74. It is possible that this species occurs more widely in the Valley, being mistaken for the commoner species, but it could also be a stray; it is usually considered a foothill and montane species. It flies with *ausonides* at 1000 feet in both the Vaca Hills and Sierra foothills.

Colias (Zerene) eurydice Boisduval. — California Dog-Faces were unusually common in the foothills in 1974. Two males were taken at Beach Lake, Sacramento Co., iii.13 and iii.21. The usual host, *Amorpha*, has not been noted there.

Lerodea eufala Edwards. — One of the rare spring emergents was taken at the American River, Sacramento Co., iv.28.74. The main summer emergence was very late, first observed viii.19, not seen at Davis until viii.31.

The addition of *N. milberti*, *C. dumetorum*, and *E. hyantis* to the Valley list raises the total fauna to 65 species.

SUISUN MARSH

The following records are additions to Shapiro, 1975c.

Euphydryas chalcedona Doubleday. — Four seen on vi.7.74, including a female. Despite this, there is no reason to believe this species breeds in the Suisun Marsh.

Phyciodes campestris Behr. — Much commoner in 1974 than in 1973, but seen only from ix.5-x.19. Clearly associated with *Aster chilensis* ssp. *lentus*, as earlier reported, and successfully reared in the laboratory on *A. chilensis* ssp. *chilensis* Nees. The distinctive Suisun facies was consistently maintained in both wild and reared individuals.

Nymphalis californica Boisduval. — Frequent in 1974. Seen on ii.23, iii.9, and iv.2. On vi.7 about 1000 seemingly fresh individuals flew across the marsh headed ENE between 1200-1500 hours. Their flight was very steady and strongly directional. Migrations oriented toward the N were observed the same week in the North Coast Ranges and at Donner Pass.

Limenitis bredowii californica Butler. — A second stray, female, ix.28.74.

**Glaucopsyche lygdamus behrii* Edwards. — Apparently resident on landfill near the Marsh, associated with a fencerow population of *Lathyrus jepsoni jepsoni*, the endemic Suisun subspecies of this plant. Collected on iii.9 and iii.20.74.

Brephidium exilis Boisduval. — In 1974 was still emerging on xii.24.

Battus philenor hirsuta Skinner. — Two additional strays, viii.6 and ix.5.74.

**Erynnis propertius* Scudder and Burgess. — One male and one female both in good condition, taken on celery blossoms in the Marsh on iv.11.74. Presumably strays from oak woodland in the nearby hills.

**Poanes melane* Edwards. — Fresh male, in a shrub thicket, ix.5.74. The origin of this individual is unknown.

Ochlodes yuma Edwards. — John H. Lane took a fresh male at the Suisun City marina x.8.74, the latest this species has been recorded in the Marsh.

The additions of *G. lygdamus*, *E. propertius*, and *P. melane* raise the Suisun species total to 43.

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AN ECOLOGICAL STUDY OF
THE BUTTERFLIES OF
THE SIERRA DE TUXTLA
IN VERACRUZ, MEXICO¹

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FRONTISPIECE

Author in Montane Rain Forest on Volcán San Martín Tuxtla, August 1962, 3,500 feet. Photograph by R. F. Andrie.

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Many persons have contributed to and assisted me in the preparation of this work and I wish to express my sincerest appreciation to them all. However, I feel that certain individuals deserve a special acknowledgment and so I wish to enumerate them. They are: Mr. and Mrs. J. M. Lind and family and Dr. and Mrs. R. F. Andriele and family for living accommodations, the wonderful hospitality that they extended to me during my residence in the Sierra, and for numerous other services subsequent to my visits; the Department of Entomology at Louisiana State University for financial assistance during my 1963 and 1965 expeditions to Mexico; F. M. Brown, H. K. Clench, R. M. Fox, W. S. McAlpine, W. J. Reinthal, E. C. Welling, and K. H. Wilson for butterfly determinations and assistance with numerous problems in butterfly systematics; V. E. Rudd and her associates at the United States National Museum for plant determinations; T. Escalante (Mexico City) for making his extensive collection of Mexican butterflies available to me; M. S. Blum for his supervision and guidance during the course of this study; H. B. Boudreaux, W. J. Harman, G. H. Lowery, Jr., L. D. Newsum, and J. S. Roberts for criticism and suggestions regarding this manuscript; and, lastly, Mrs. G. G. Wynn for her assistance in proofreading the manuscript and numerous other tasks.

TABLE OF CONTENTS

	Page
TITLE PAGE	1
ACKNOWLEDGMENTS	4
TABLE OF CONTENTS	5
LIST OF TABLES	6
LIST OF FIGURES	7
LIST OF PLATES	8
ABSTRACT	9
CHAPTERS	
I. INTRODUCTION	11
II. TOPOGRAPHY AND GEOLOGY	15
III. CLIMATE	19
IV. VEGETATION	21
V. ACCOUNTS OF BUTTERFLY SPECIES IN THE SIERRA DE TUXTLA	51
Plan of the Species Accounts	51
Accounts	55
Family Papilionidae	55
Family Pieridae	62
Family Ithomiidae	70
Family Danaidae	74
Family Satyridae	75
Family Nymphalidae	81
Family Lycaenidae	105
Family Riordinidae	120
VI. CORRELATION AND SYNTHESIS	129
Biotic Relationships	129
Faunal-Floral Relationships	141
Climatic Relationships	145
Faunal Relationships	147
REFERENCES CITED	156
APPENDICES	159
APPENDIX A	159
APPENDIX B	171

LIST OF TABLES

	Page
I. Plant Formations in the Sierra de Tuxtla	23
II. Plant Formations and Associated Butterflies in the Sierra de Tuxtla	131
III. Life Zones and Corresponding Plant Formations in the Sierra de Tuxtla	140
IV. Genera of Butterflies Collected in the Sierra de Tuxtla within Forests with Closed Canopies	142
V. Species of Butterflies Collected in the Sierra de Tuxtla Known to Occur within the Borders of the United States	148
VI. Comparison of Butterfly Genera Common to the Sierra de Tuxtla, the United States, and the Neotropical Regions	150
VII. New Butterfly Records for the Sierra de Tuxtla (excluding Endemics)	152
VIII. Butterflies Endemic to the Sierra de Tuxtla	155

LIST OF FIGURES

	Page
1. Location map of the Sierra de Tuxtla	12
2. Vegetation of the Sierra de Tuxtla	24

LIST OF PLATES

	Page
Frontispiece	
1. Lago Catemaco	14
2. Volcan San Martin Tuxtla	16
3. Volcan Santa Marta	18
4. Volcan San Martin Pajapan	20
5. Lower Montane Rain Forest	26
6. Montane Rain Forest or Cloud Forest	28
7. Gum-oak forest	30
8. Montane Thicket	32
9. Elfin Woodland	34
10. Semi-Evergreen Seasonal Forest	36
11. <i>Bursera-Sabal-Orbignya</i> Forest	38
12. Savanna	40
13. Deciduous Woodland	42
14. Pine-oak Forest	44
15. Littoral Woodland	46
16. Swamp Forest	48
17. Mangrove Woodland	50
18. Recently Abandoned Milpa	52
19. Pasture	54
20. Hedgerow	56

ABSTRACT

The Sierra de Tuttl is a small and isolated volcanic mountain range along the Gulf coast of southern Veracruz, Mexico. Because of the geographic isolation, the range affords excellent conditions for distributional and ecological investigations. The present study is the first comprehensive report of the butterfly fauna of the range or for any geographic unit within the Neotropics.

Fifteen months (representing all seasons of the year) were spent in the field during 1962, 1963, and 1965. The various relatively widespread plant communities were classified into 16 distinct types or formations. All of these formations were sampled for butterflies and a total of 3,893 specimens representing 359 species, 133 genera, and eight families were collected. Of these species, 40 are recorded from the Sierra for the first time; these include ten range extensions within the state of Veracruz, 18 new state records, nine new national records, three new species, and one new subspecies. All 359 species are listed in the species accounts along with the field data—complete (number of specimens, locales and altitudes, and collection date) for those species that represent new records for the Sierra but condensed (number of specimens and only ranges in altitude and collection dates) for those species recorded previously from the Sierra.

Various relationships between the butterfly fauna and the environment are discussed. First, an analysis of the plant formations with their indicator and characteristic butterfly species indicates that life zone boundaries within the Sierra are vague but still definable. The Sierra can be divided into two major zones—an Upper Tropical Zone and a Lower Tropical Zone. Furthermore, the data indicate that the Lower Tropical Zone can be subdivided into a humid and an arid component.

Second, the majority of the butterfly species were found in the Lower Tropical Zone in the open and relatively open plant formations whereas very few species (principally members of the Ithomiidae and Satyridae) were found in the dark interiors of the forests. Because of the Sierra's relatively low altitude and relatively uniform rainfall, it is suggested that the principal governing factor determining butterfly areal and altitudinal distributions is the plant formation.

Third, although butterfly zoogeography is not sufficiently advanced to enable one to determine the origins of most genera and species groups, the majority of the genera (97%) and species (97%) found within the Sierra's boundaries appear to have their affinities with forms further south; consequently, the butterfly fauna is essentially Neotropical.

Fourth, although the climate in the Sierra is relatively mild and uniform, enough diversity exists to produce significant variations in the butterfly populations. In general, populations of most species reached maximum densities in late summer and early fall and their minimum densities in winter and spring. In addition, daily population densities were greatest between the hours of 10:00 A.M. and noon.

Fifth, butterfly endemism proved to be comparable to endemism in other groups; three species, one subspecies, and one form (probably a good subspecies) are endemic to the Sierra de Tuttl.

I. INTRODUCTION

The Sierra de Tuxtla or Tuxtla Mountains (Tuxtla being the Spanish corruption of the Aztec "Toxtli" meaning rabbit) is a rather restricted highland of volcanic origin situated between $18^{\circ}10'$ and $18^{\circ}45'$ N latitude and $94^{\circ}42'$ and $95^{\circ}27'$ W longitude on the Gulf Coastal Plain of the state of Veracruz in the Republic of México (Fig. 1). The range trends northwest-southeast with areal dimensions of approximately 55 by 30 miles and is isolated from any other highland (the nearest being the Sierra Juárez in the state of Oaxaca approximately 90 miles away) by the Veracruz lowlands, principally the drainage basins of the Papaloapan and Coatzacoalcos rivers. The Sierra is composed of numerous ridges and volcanic cones and peaks of which four attain elevations in excess of 3,000 feet, the maximum elevation being 5,450 feet. These volcanic extrusions encircle a central basin containing the picturesque Lago Catemaco, the third largest lake in Mexico (Plate 1).

When man first entered and began to settle the Sierra is still unknown. Sears (1952) states that artifacts dating from approximately 1500 to 500 B.C. and probably Olmec in origin were found in archeological sites in and around the range. The Spaniards reached the Sierra a few years subsequent to their arrival in Mexico—ca. 1522 (Melgarejo Vivanco, 1960). Today the area of approximately 2,700 square miles is moderately populated with both Mexicans and Indians, (Popolucas and Aztecs), the total population in 1960 being approximately 145,000 (Andrle, 1964). The people are engaged mainly in subsistence agriculture, which includes the cultivation of corn, coffee, tobacco, and citrus fruits. Because of the rather long history of settlement and cultivation, relatively few undisturbed areas still exist. These are found principally on the windward (Gulf facing) slopes of the major volcanoes and on the leeward slopes above elevations of 2,500 to 3,000 feet.

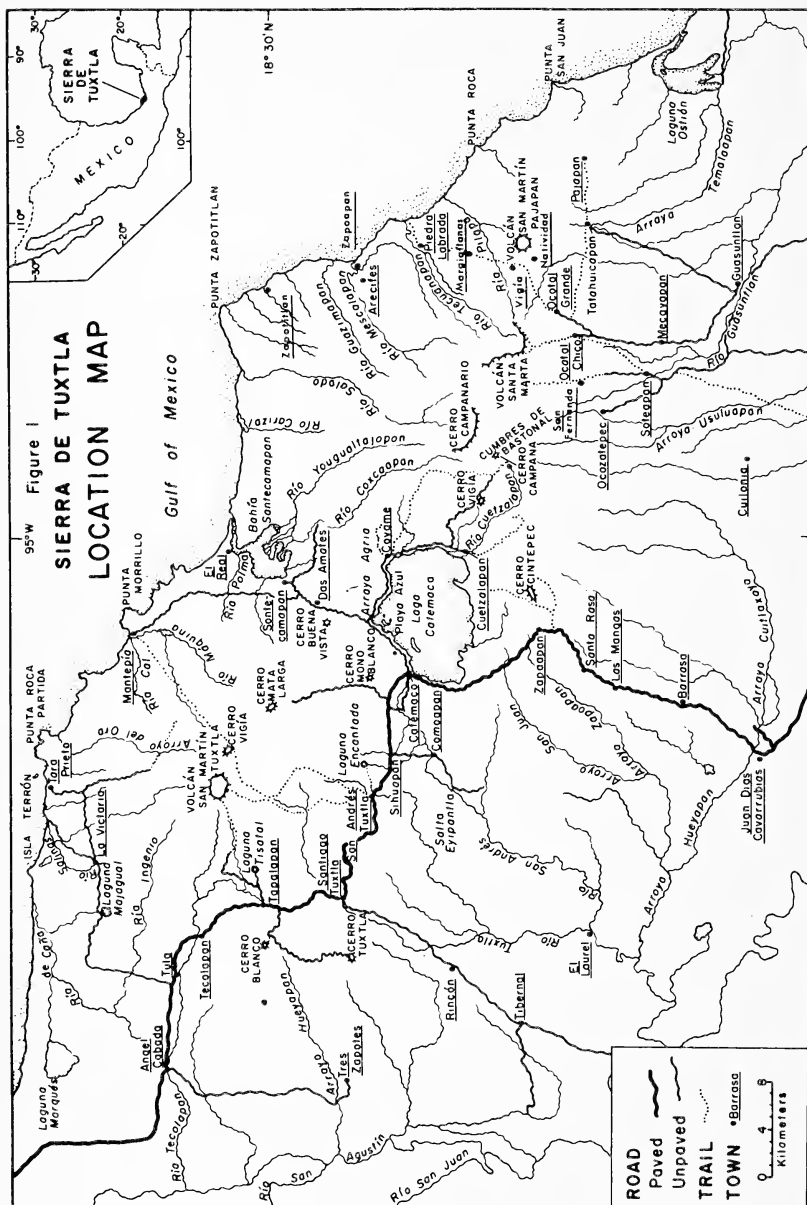


FIGURE 1
Location map of the Sierra de Tuttle. Map modified from that of Andrade (1964). Basic map used with the permission of the author.

Scientific studies in the Sierra have been very limited and brief; biological investigations have been confined almost exclusively to the vertebrate fauna of the Lago Catemaco basin and the slopes of Volcán San Martín Tuxtla. Avian and mammalian studies include those of Sclater (1897), Wetmore (1943), Goldman (1951), Davis (1952), Amadon and Eckelberry (1955), Edwards and Tashian (1959), and Andrlé (1964). Herpetological studies include those of Firschen (1950), Firschen and Smith (1956), and Pyburn (1963, 1964, 1966). Previous studies on arthropods are limited to a single paper on opilionids (Goodnight and Goodnight, 1959).

My interest in the Sierra de Tuxtla began in 1961 because of R. F. Andrlé, a fellow graduate student who previously had visited the range and who at the time was preparing for a 12 month return visit in early 1962 to study in detail the mammalian and avian faunas. Andrlé's enthusiasm about the Sierra coupled with the fact that comprehensive studies on the bionomics of Neotropical butterflies are practically nonexistent, convinced me that the Sierra de Tuxtla would be an ideal study area for me. So in June 1962 and with Andrlé as a field partner, I began my investigation of the Sierra's butterfly fauna. During this first study period (June through mid-December) my main base of operations was located at Playa Azul on Lago Catemaco. From that locale I directed my studies to the Volcán San Martín Tuxtla massif and the Lago Catemaco-Bahía Sontecomapan areas. Two incidental papers (Ross, 1963, 1964b) resulted from this endeavor. The following year, June through August 1963, I made a return visit to the Sierra and established a base at Ocotál Chico. During this period my studies were directed to the Volcán Santa Marta massif. Three incidental papers (Ross, 1964c, 1964d; Hepburn and Ross, 1964) resulted from this study. In 1965 (February through July) I revisited the Ocotál Chico site and expanded my investigation of the region to include the Volcán San Martín Pajapan massif. One incidental paper resulted from this 1965 trip (Ross, 1966). Transportation during all of the study periods was provided by four-wheel drive vehicles, trucks, mules, power boats, canoes, and my own two feet.

This dissertation is based on an assemblage of 3893 butterfly specimens collected during a total of 15 months of personal field



PLATE 1

Lago Catemaco, view toward the western margin. August 1962, 1,100 feet.
Photograph by R. F. Andrie.

work in the Sierra. In sections II (TOPOGRAPHY AND GEOLOGY) and III (CLIMATE) I have relied heavily on information presented by Andrieu (1964) and the reader is referred to that work for additional and more detailed discussions of those topics.

II. TOPOGRAPHY AND GEOLOGY

The Sierra de Tuxtla is an isolated mountain mass dominated by four relatively large volcanoes. To the north these slope rather steeply down to the Gulf of Mexico. To the South, West, and East they slope more gently down to the Gulf Coastal Plain. All slopes are deeply dissected and a radial erosion pattern is very evident. The Sierra can be divided by the basin of Lago Catemaco into a northwest and a southeast massif. The northwest massif is dominated by Volcán San Martín Tuxtla (5,450 feet; Plate 2) and to a lesser extent by Cerro Tuxtla (2,725 feet), Cerro Blanco (2,375 feet), and the elongate Cerro Cintepec (2,950 feet). Numerous small cones, hills, and crater lakes are common south, east, and west of Volcán San Martín Tuxtla. To the north, long, steep-sided ridges radiate down to the Gulf of Mexico. The southeast massif is dominated by Volcán Santa Marta (5,250 feet; Plate 3), Volcán San Martín Pajapan (3,750 feet; Plate 4), and Cerro Campanario (3,900 feet). The southeast section exhibits more uniformity than does the northwest section in the sense that there are very few secondary cones and crater lakes.

The numerous ravines on the slopes of the volcanoes usually contain swift-flowing, clear streams, the flow from many of which is either significantly reduced or stopped during the spring dry season. The streams usually are fed by cool, clear springs that issue from rock crevices on the upper slopes of the volcanoes. At lower elevations the streams join larger streams and rivers which in turn eventually flow into the Gulf of Mexico.

Murray (1961) states that the Tuxtla Uplift probably existed as early as Mesozoic times. He considers the uplift to be high areas of basement rock in the Mesozoic-Cenozoic geosyncline that probably was part of the arc-shaped "Tamoulipas-Yucatan archipelago." Later, this syncline sank and was subjected to Cretaceous and Tertiary deposits of blue clays and shales, tuffs, sandstones, limestones, and conglomerates, which upon later emergence of the Sierra, were partially eroded away.

Schieferdecker and Tschopp (1922) suggest that the Sierra



PLATE 2
Volcán San Martín Tuxtla. August 1962, 2,000 feet. Photograph by R. F. Andrie.

rests on a diaritic laccolith of early Miocene or Oligocene age that lifted and in places folded the Tertiary beds and from which the volcanic extrusions have emerged. These extrusions comprise most of the present-day Sierra and consist of older Pliocene deposits of an acid andesitic character upon which were superimposed basalt flows and volcanic plugs of late Pliocene age following the last marine inundation.

Andrle (1964) recognized seven principal eruption centers or zones within the Sierra. These are: Cerro Tuxtla, Cerro Blanco, Volcán San Martín Tuxtla, the Lago Catemaco Basin (including Cerros Mono Blanco, Las Animas, and Cintepec), Cerro Campanario, Volcán Santa Marta, and Volcán San Martín Pajapan. Besides these principal cerros, there are numerous subsidiary lava, ash, and cinder cones in the area, principally in the vicinity of Volcán San Martín Tuxtla. The true nature of Lago Catemaco is still debatable. Friedlaender (1923) considered it to be a caldera but Andrle (1964) suggests that it is simply a spring and stream-filled low section of the range whose southern and western borders are effectively blocked by volcanic cones and debris. Layers of ash, lapilli, and cinders are evident particularly in the Catemaco basin. Basalt bombs, pumice, and asphalt cakes are fairly common, particularly along the coast. Fine-grained olivine basalt rocks are the dominant rock type throughout the Sierra. These are evident as blocks, both large and small, and as extensive flows, which in places exhibit columnar faulting.

Only Volcán San Martín Tuxtla has a historical record of eruptions. This fact tends to support the suggestions of Friedlaender (1923) that the northwest massif is of younger geologic age than the southeast counterpart. Medel & Alvarado (1963) briefly described an eruption on October 15, 1664, which Friedlaender (1923) defined as an ash eruption with a possible restricted lava flow to the north. Mociño (1870) reported a second eruption that began in March 2, 1793 and that consisted of violent explosions, lava flows to the northeast and northwest, and ash falls that continued intermittently through September. Garcia (1835) observed fumarolic activity in the crater in 1829 but nothing more.



PLATE 3
Volcán Santa Marta. Body of water in the foreground is an artificially
created reservoir. June 1965, 500 feet.

The four major volcanoes each show well developed oval and steep-walled craters, which for the most part, are open to the north indicating the direction of major lava flows. The crater of Volcán San Martín Tuxtla has a maximum length of approximately one mile and a maximum depth of approximately 600 feet. The crater of Volcán Santa Marta has a maximum length of approximately one and a half miles and a maximum depth of approximately 500 feet. Cerro Campanario and Volcán San Martín Pajapan have craters smaller and shallower than those of Volcáns San Martín Tuxtla and Santa Marta.

III. CLIMATE

The Sierra de Tuxtla is characterized by rather uniform year-round temperatures and seasonal rainfall. This rather mild climate is a result of the moderating effect of the Gulf of Mexico. Andrle (1964) lists temperature and precipitation data for six stations in the Sierra. Unfortunately, all of these stations are in a relatively narrow zone on the southern slopes of the Sierra and hence, the data can be used only to illustrate general trends. April and May usually are the warmest months and January and February the coolest. The average annual temperature is approximately 75.5°F (average elevation of 955 feet). The average mean for the coldest month is 68°F. The lowest temperature recorded at any station (San Andrés Tuxtla, 1,188 feet, 32 years of data) was 44.2°F. Medel & Alvarado (1963) reported that on February 9 and 10, 1899, the peak of Volcán San Martín Tuxtla was covered with ice; thus freezing conditions are not unknown on the peaks of the highest volcanoes. Low temperatures usually occur between October and April after the passage of a mass of cold air that moves across the Gulf from the north or northeast. These fronts, which are called "nortes" by the local inhabitants, vary in intensity and duration, some being weak and lasting for only two or three days, others somewhat stronger and lasting for as long as seven days.

Precipitation is variable with two pronounced seasons—a wet season from June through January (maximum rainfall in July and October) with usually a slight decrease in August, and a dry season from February through May (minimum rainfall in March and April). Most precipitation during the winter months is associated with the passage of fronts. Most summer and fall precipitation occurs during thundershowers in the night and early morning. Andrle's climatic data indicate that rainfall is



PLATE 4
Volcán San Martín Pajapan. May 1965, 2,600 feet.

principally an orographic type and varies considerably between each station and even from year to year at any single station. The minimal early average for any station is 69 inches at Guasuntlan (elevation 595 feet) and the maximal yearly average is 163 inches at Coyame (elevation 1,122 feet). Rainfall above elevations of 1,500 feet on the Gulf slopes is probably in excess of 170 inches per year, and the peaks of the principal volcanoes conceivably receive upwards of 200 inches per year because of the orographic effect.

The cloudiest months are December, January, and July; the least cloudy are March, April, and May.

Since the mean temperature of the coldest month is greater than 64.4°F and the mean precipitation of the driest month is greater than 2.4 inches, the Sierra falls within the "Tropical Rain Forest Climate" (Af) of Koppen (1936).

IV. VEGETATION

The Sierra de Tuxtla lies within (but near the northern border of) the Neotropical Realm of Wallace (1876) and represents the most northern extension of the relatively uninterrupted belt of tropical rain forest that extends (in climatically favorable areas) from southern Mexico through Central America and far into South America (Leopold, 1950; 1959). Hence the floristic composition of the region is basically tropical with most components being related to plant groups further south. This tropical composition coupled with the fact that the Sierra represents a relatively small geographic area (approximately 2,700 square miles) would lead one to the conclusion that the flora of the region is rather homogeneous. Such a conclusion, however, would be completely erroneous because the Sierra exhibits a considerable diversification in vegetation. This diversity is a result of many factors of which some of the most important include: altitudinal zonation from sea level to a maximum elevation of 5,450 feet resulting in temperature and rainfall gradients; differences in the composition and ages of soils due to differential weathering and variances in age of parent material; the long axis of the range in respect to the prevailing winds resulting in relatively heavy precipitation on the Gulf facing slopes and a slight rain shadow effect on the leeward slopes; and

the agricultural practices of man resulting in the presence of all stages of plant succession.

Plant Formations

In attempting to define the habitats of butterfly species in the Sierra, a more subtle ecological division that either "life zone" or "biotic province" had to be chosen. Because of the Sierra's numerous and frequently widely distributed plant communities, I decided to employ a habitat classification based on plant formations.

Andrle (1964) in his investigation of the Sierra differentiated between ten distinct types of vegetation. However, because of the broadness of many of his terms I have found it necessary to modify this classification. This was accomplished by correlating (where possible) the apparent climax types with those as outlined by Beard (1944; 1955). When no correlations were apparent, e.g., the various seral communities and the oak and pine communities, I have erected new categories, being careful not to employ any of the Beard terminology. The result of this effort is that I recognize 16 distinct formations in the Sierra (Table 1). The geographic locations of the major types are illustrated in Figure 2. In actuality the boundaries between each type and the next are rather arbitrary for oftentimes relatively wide transitional zones or ecotones exist between formations.

(to be continued)

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Volume 14

Number 2

May, 1976⁵

IN THIS ISSUE

- | | | |
|---|---------------------|-----|
| The genetics of subspecific phenotype differences
in <i>Pieris occidentalis</i> Reakirt and of variation
in <i>P. o. nelsoni</i> W. H. Edwards (Pieridae) | Arthur M. Shapiro | 61 |
| Early stages of <i>Phyciodes pallida</i> , <i>P. orseis</i> ,
and <i>P. mylitta</i> (Nymphalidae) | James Scott | 84 |
| Recent captures of <i>Anthocharis cethura catalina</i>
Meadows | Larry J. Orsak | 85 |
| Old Timers | John Adams Comstock | 90 |
| Why do California Tortoiseshells migrate? | Arthur M. Shapiro | 93 |
| Early work on the Megathymidae | John Adams Comstock | 98 |
| Supplementary records of butterflies in the
Sacramento Valley and Suisun Marsh,
lowland central California | Arthur M. Shapiro | 100 |
| An ecological study of the butterflies of
the Sierra de Tuxtla in Veracruz, Mexico | Gary N. Ross | 103 |

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COURTSHIP AND MATING BEHAVIOR
OF THE FIERY SKIPPER, *HYLEPHILA PHYLAEUS*
(HESPERIIDAE)
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ABSTRACT

The courtship and mating behavior of *Hylephila phylaeus* (Hesperiidae) was studied by introducing dead and live tethered wild and laboratory reared females to wild males in the field. The hypothesis that wing movement elicits the male's initial investigative response in this species was tested. Entire courtship sequences resulting in successful matings were obtained with 18 live virgin females, indicating that males are less responsive to previously mated females.

INTRODUCTION

The problem of locating and successfully mating with a conspecific is of primary importance in the perpetuation of a species. Not only must potential mates recognize one another as opposed to closely related species, but a synchronization of reproductive cycles must occur so as to bring members of the opposite sex together at the proper time of year. Only by studying the courtship and mating systems of individual species can theories pertaining to the significance of various aspects of such systems be validated.

The present study deals with the courtship and mating system of a Lepidopteran, the fiery skipper, *Hylephila phylaeus* (Hesperiidae). This species is abundant in the Sacramento Valley of California, where it is multiply brooded, having up to five generations per year. The larval host is Bermuda grass, *Cynodon dactylon* (Gramineae). *H. phylaeus* can be classified as a perching species as defined by Scott (1974c), i.e. males perch on projecting objects such as leaves, pieces of paper, and tall blades of

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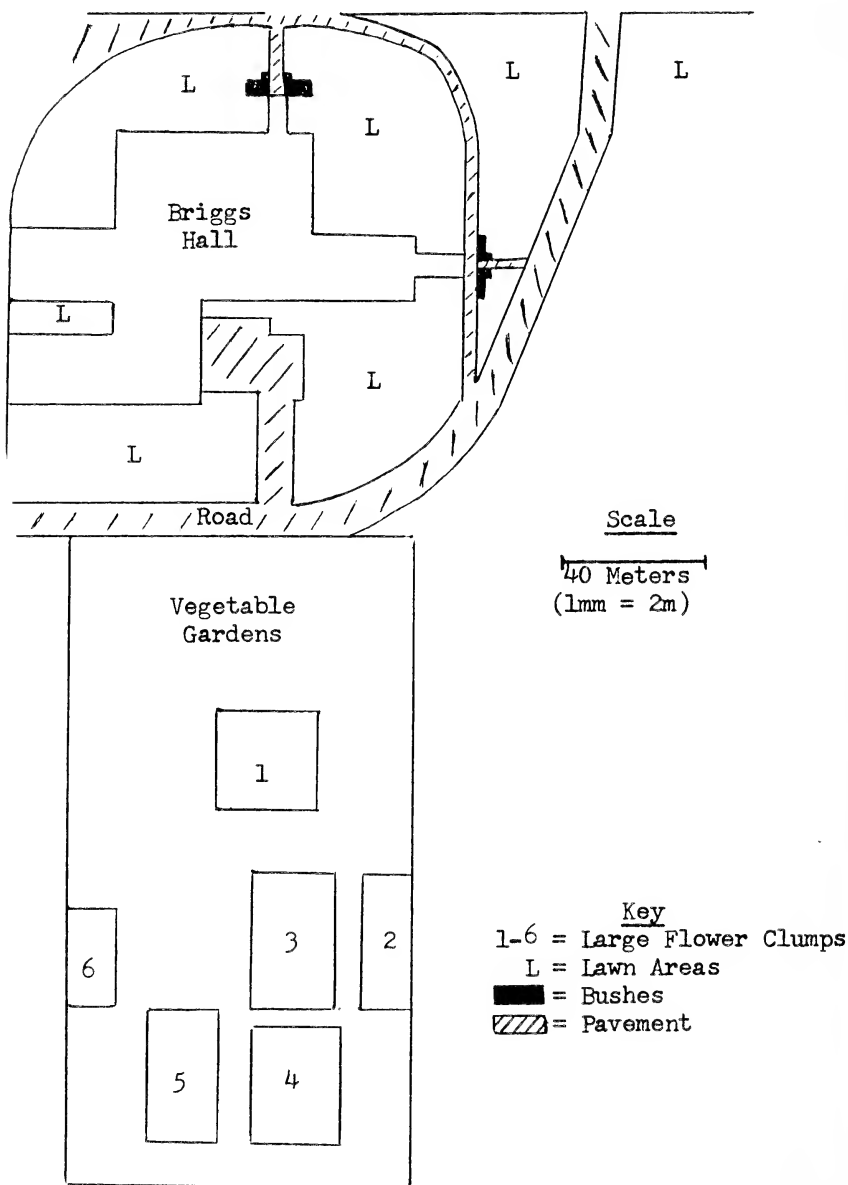
Map of Study Area (34,000 square meters)

Fig. 1.—Map of Study Area (34,000 square meters)

grass on lawns and vacant lots in residential areas. Perching males fly towards and "investigate" moving objects such as other butterflies of the same or different species, other insects, and bits of leaves blown by the wind. The hypothesis that movement (specifically wing fluttering movement) elicits the male investigative response in this species was tested in the field.

MATERIALS AND METHODS

The study was conducted on the University of California, Davis campus throughout the periods of September to November, 1973 and June to December, 1974. The 34,000 square meter study area consisted of a 12,300 square meter lawn area of *Cynodon dactylon*, *Poa pratensis*, *Agrostis alba*, and *Festuca rubra*, which was separated by a road (10 meters in diameter) from a 21,700 square meter flower and vegetable garden that served as a food source for adult *phylaeus* (see Map Fig. 1). Male perching and investigative behavior were observed on the lawn area, while courtship and mating behavior experiments were conducted in the vegetable gardens because of the greater density of *H. phylaeus* there.

In order to determine the behavioral components involved in a complete courtship sequence, dead and live wild male and female *H. phylaeus* were presented to wild males in the field. A modification of the technique devised by Tinbergen et al. (1942) was used: butterflies were cooled for about ten minutes at 12°C so as to facilitate handling, and a quick-drying epoxy cement was applied to the dorsal surface of the thorax while a fine piece of fishing line was held in position until the glue dried (about three minutes). The fishing line was then attached to a rod which could be dangled in front, above or to the side of males at a distance of up to 1.8 meters from the observer. When fishing line was properly mounted, no difference from normal rapid flight movement was observed, except that individuals could not fly farther than a 1.8 meter diameter circle around the observer.

In a second group of experiments, laboratory reared females and males were presented in the same manner to wild males in the field in order to determine whether different results could be obtained with females known to be virgin. Results were recorded by notes and through use of a portable cassette tape recorder.

Table 1. 1973 Experiments with Tethered Wild Males and Females Presented to Wild Males in the Field (n = # males investigating or touching tethered skipper; N = total # males to which tethered skippers were presented; * = tethered skipper not flying, data discarded).

#	Tethered Females Presented to Wild Males				Tethered Males Presented to Wild Males				Tethered Eufala Presented to Wild Males			
	Male Investigated		Male Touched		Male Investigated		Male Touched		Male Investigated		Male Touched	
	n	N	%	n	N	%	n	N	%	n	N	%
1	10	12	83	2	12	16.7	9	10	90	2	10	20
2	10	11	91	4	11	36.4	8	10	80	1	10	10
3	9	10	90	1	10	10	7	10	70	0	10	0
4	8	10	80	0	10	0	8	10	80	2	10	20
5	9	10	90	2	10	20	10	10	100	1	10	10
6	10	10	100	0	10	0	9	10	90	0	10	0
7*	3	10	30	0	10	0	-	-	-	-	-	-
8*	0	10	0	0	10	0	-	-	-	-	-	-
Total	56	63	89	9	63	14.3	51	60	85	6	60	10
							27	30	90	3	30	10

(No significant difference at .05 level between female, male, and eufala tethered skippers, using the t-test of difference between two means).

RESULTS

1973 Experiments with Wild Females and Males Presented to Wild Males

All experiments with dead male and female *phylaeus* failed to elicit courship behavior from wild males in the field. 13 dead females and 15 dead males presented to 10 wild males apiece elicited no responses, even when tethered skippers were dangled from fishing line directly in front of males. 2 dead females elicited an approach response, investigative behavior, from one of ten males apiece. In both instances, males immediately departed without touching or following the females. As a control, all tethered animals were also presented to 10 wild females apiece, and negative results were obtained in all cases.

Experiments with live *phylaeus* yielded more positive results on the preliminary phases of courtship. Data from 8 female and 6 male *H. phylaeus* were obtained. Both males and females elicited investigative behavior from wild males. When a tethered skipper was moved past a male at a distance of 0.3 to 0.6 meters, the male usually flew toward and often touched it with his head and antennae. A few males followed the tethered skipper for several feet, but most immediately departed, returning to an area near their original position. All tethered animals were presented to 10 wild females apiece, and no responses were elicited.

Five *Eufala* skippers, *Lerodea eufala*, were used in another group of experiments. In this species, the sexes are phenotypically alike, both being an overall brown-gray color with a peppering of small white spots on the upperside of the forewing. Investigative behavior and touching behavior were again elicited when live tethered *eufala* were presented to wild male *phylaeus*, and no responses were elicited when presented to wild females.

Results suggest that the fluttering of the wings during flight is a stimulus necessary to induce investigative behavior in males, since in all but two instances where a tethered skipper did not flutter its wings but merely hung at the end of the line, males did not respond. Differences in responses to female and male *phylaeus* and *eufala* were not significant at the 95% level using the t-test of difference between two means. This further substantiates the hypothesis that the fluttering of the wings may be more important than color or scent in initiating the first stages of courtship in *H. phylaeus* (Table 1).

1974 Experiments with Virgin Females and Males Presented to Wild Males

Results obtained in the 1974 experiments support the hypothesis that the fluttering of the wings is an essential stimulus to elicit investigative behavior in males. 16 females did not fly when presented to 10 males apiece, and subsequently failed to elicit a response in all 10 males. One female that failed to flutter its wings did elicit investigative behavior in three of 10 males, while two more non-flying females stimulated approaches in one of 10 males apiece. It was also found that feeding males usually failed to respond to tethered skippers. Out of a total of 71 trials with 16 female *phylaeus*, only 3 feeding males were stimulated to investigate; the other 68 males continued to feed.

Because no complete courtship sequences could be induced in the 1973 experiments with wild females, it was hypothesized that perhaps only virgin females could provide the correct stimuli necessary to elicit a sequence resulting in a successful mating. Therefore, in 1974, laboratory reared virgin females were used in the experiments. As a control experiment, 10 laboratory reared virgin males were also presented to wild males in the field; results were identical to those of 1973, where only the first phase of courtship, investigative behavior, was elicited. Experiments with virgin females, however, produced 18 successful matings. A description of the various phases in the courtship sequence of *H. phylaeus* is as follows:

Phase 1 — Investigative Behavior: the male flies toward and may touch a passing female.

Phase 2 — Settling Behavior: the male lands behind the female as she settles on a leaf, flower, or the ground.

Phase 3 — Head-Wing Behavior: the male, while situated at the rear of the female, thrusts his head between the female's hindwings, touching the upper surface of her wings and the rear of her abdomen with his head and antennae; males often thrust themselves so far forward that they are able to touch the upperside of the female's forewings.

Phase 4 — Fluttering Behavior: the male rapidly flutters his wings while moving laterally to the female and/or in front of her.

Phase 5 — Curving Behavior: the male, in a position posterior to the female, curves his abdomen in a U-shaped arc, so that his genitalia are in close proximity to the female's; the male genitalia are often extruded.

Phase 6 — Coupling Behavior: the male clasps the female with his harpes and apparently inserts his aedeagus into the female; after several seconds to several minutes, the male moves his body around so that he is facing in the opposite direction from the female (their bodies form a 180° angle).

Phase 7 — Uncoupling: copulation was terminated from 40 to 72 minutes after coupling except in one instance, when the mating pair separated after 27 minutes; it is not known whether a spermatophore was transferred or not, since the female flew away immediately after uncoupling. After separating, the male and female of all pairs observed either began feeding or flew away.

In the 18 successful courtships observed, overt female sexual behavior was minimal. The female usually remained stationary where she had settled, occasionally moving her antennae or walking forward several centimeters. In a few instances, females were observed to extrude genitalia, although this behavior also occurred during unsuccessful courtships. Shapiro (1970) proposed that such behavior in Pierid butterflies is part of a rejection display by unreceptive females. An identical display in Heliconiid butterflies, however, appears to have a pre-copulatory function, since in this group, the extrusion of the genitalia is related to pheromone release (Crane, 1957).

The duration of successful courtships prior to coupling ranged from ten seconds to three minutes and 30 seconds. Most were of short duration, and only five of 18 were longer than 40 seconds. Similar results were obtained by Brower et al. (1965), who found that the mean duration for 266 courtships in *Danaus gilippus berenice* was 40.4 seconds.

There was considerable variation in the sequence of phases as well as the repetition of phases among individual courtships. Nine courtships were single-phased sequences, while the other nine had sequences with repetitious phases. All but three courtships began with investigative behavior followed by the settling phase (Table 2).

Only one successful wild courtship as opposed to 208 unsuccessful wild courtships was ever observed. The duration of the courtship was 15 seconds, and the duration of time in copula was 40 minutes. The courtship was single-phased and was sequentially analogous to successful courtships in the experiments with laboratory reared virgin females.

Seven cases of carrying pair behavior were observed. In all cases, the female flew while carrying the quiescent male. Such behavior occurred only when the pair was disturbed in some way, such as by other males attempting to court the female or when touched by the investigator.

Table 2. 1974 Experiments with Virgin Females Presented to Wild Males in the Field - Sequence of Phases in Successful Courtships.

Female #	Sequence of Phases
1	1-2-4-5-6-M
2	1-2-3-4-5-6-M
3	1-2-5-6-M
4	1-2-5-4-6-M
5	1-2-5-6-4-M
6	1-2-5-4-6-M
7	3-4-5-6-M
8	1-2-3-4-5-6-M
9	1-2-3-5-6-M
10	1-2-5-4-6-P-5-6-P-6-M
11	1-2-5-4-3-5-6-M
12	1-2-4-3-5-6-P-5-6-4-Fl-2-5-6-M
13	2-5-3-4-6-4-P-5-4-6-S-P-3-4-5-4-6-M
14	1-2-5-6-P-5-6-M
15	1-2-4-5-6-P-5-6-P-5-6-4-M
16	1-2-5-6-4-P-6-3-4-M
17	1-2-5-3-4-S-6-P-5-3-4-S-5-3-4-S-6-5-3-4-6-M
18	2-4-3-4-5-6-FD-2-6-P-5-6-P-4-6-M

Courtship Sequences
with Single Phases

Courtship Sequences with
Repetitious Phases

Key

- 1 = Investigative Behavior
- 2 = Settling Behavior
- 3 = Head-Wing Behavior
- 4 = Fluttering Behavior
- 5 = Curving Behavior
- 6 = Coupling Behavior
- M = Successful Mating
- P = Female Pulled Away
- S = Female Shuddered
- Fl = Courtship Disrupted by Another Male
- FD = Female Deserted

Unsuccessful Courtships with Virgin Females

The courtship sequence can be terminated by either the male or the female after any of the first six phases in any of several ways. The most common cause of unsuccessful courtship was disruption by other males, which resulted in the courting male leaving the female and flying after the other male. Such investigative behavior often resulted in "chases" between two or more males to areas far removed from the origin of the encounter. 41 out of 88 unsuccessful courtships ended in this type of disruption behavior.

36 out of 88 courtships ended in male desertion behavior, where the male departed to a nearby flower or leaf. Such behavior may be elicited by a female rejection display called shuddering behavior, in which the female rapidly flutters the forewings and hindwings, which are opened at about a 45° angle from one another. Shuddering could be elicited either by head-wing behavior, fluttering behavior, or curving behavior and was often accompanied by movement a short distance away from the male. 28 of 36 courtships terminating by male desertion occurred after the female had shuddered once or several times.

These observations are in sharp contrast to the successful matings observed, where there were 16 out of 18 courtships in which the female did not shudder. It may be significant to note that the two females that did not shudder had repetitious courtship sequences, and that neither shuddered during the final sequence culminating in a successful mating.

Another female display which may be a rejection is the raising of the abdomen up and away from the male's genitalia during coupling. In all cases such pulling away behavior resulted in an uncoupling of the pair.

Courtships were also terminated by female desertion, where the female flew away from the male to another area. Only 11 out of 88 courtships ended in this manner (Table 3).

Unsuccessful courtships with virgin females were longer than unsuccessful courtships with mated females. Only the first phase of courtship, investigative behavior, was elicited by mated females, while virgin females elicited at least one of the later stages of courtship (settling, head-wing, fluttering, curving).

Table 3. 1974 Experiments with Virgin Females Presented to Wild Males in the Field - Causes of Termination of Unsuccessful Courtships (in # of Observations).

Female Rejection Display	Disruption by Other Males	Male Desertion	Female Desertion	Total
Shuddering	17	28	7	52
Pulling Away	3	4	0	7
No Rejection Display	21	4	4	29
Total	41	36	11	88

DISCUSSION

Courtship and mating systems of insects have been shown to consist of progressive exchanges of stimuli between males and females; one partner's response to a stimulus elicited by the other releases the next response, and so on (Frings and Frings, 1958; Perdeck, 1957; Crane, 1957; Baerends, 1959). In *Hylephila phylaeus*, the initial investigative response of males appears to be elicited by movement, specifically the fluttering of the wings. Color of the wing does not appear to play a significant role, since males were equally attracted to both male and female *phylaeus*, despite the pronounced sexual dimorphism in this species, as well as to the darker *eufala* skippers. Size may possibly be a factor, although male *phylaeus* were occasionally seen to investigate larger butterfly species, such as *Vanessa cardui*, *V. carye*, *Colias eurytheme*, and *Pieris rapae*.

Magnus (1958) obtained similar results with *Argynnis paphia* (Nymphalidae). He proposed that the fluttering of the wings itself was not the decisive factor, but rather the rapid alteration of color versus absence of color when the wings are fluttered. He found that the intensity of the male response rose in direct proportion to the speed of color alteration. It is possible that a similar response may occur in *H. phylaeus*, since experiments thus far indicate that the fluttering motion of the wings is essential in eliciting a male response.

The investigative reaction appears to be related to the mate-locating system of various butterfly species: in perching species, the female must fly past the male to attract his attention; in patrolling species, it is the male that must fly past and locate non-flying females (Scott, 1974c). It would thus appear that color might be an important stimulus to the patrolling male, while the perching male would be more attracted to movement or quick flashes of color from fluttering wings. Thus far, the available data substantiates this hypothesis. In the perchers *Hypolimnas misippus* (Stride, 1957, 1958a and b), *Neominois ridingsii*, *Hesperia pahaska*, *Ochlodes snowi*, *Lycaena arota*, and *Amblyscirtes simius* (Scott, 1973a,b; 1974a), the first phase of courtship is elicited by movement of the female past the stationary male. In the patrollers *Argynnis paphia* (Magnus, 1958), *Erebia epipsodea* (Brussard and Ehrlich, 1970a,b), *Hypaurotis corydon* (Scott, 1974b), and *Pieris rapae* (Obara, 1970), color of the female appears to be of primary importance in attracting males. In the patroller *Danaus gelippus berenice*,



Fig. 2.—Settling Behavior of *Hylephila phylaeus* During Courtship Sequence (Male Lands Behind Female).

however, Brower et al. (1965) stated that males are initially attracted to the female by seeing her in flight or while she is fluttering on herbage. Such behavior may be an artifact due to the procedure used by the investigators—females were released by hand into the air and all females that did not fly past the male were discarded from the results.

In *H. phylaeus*, the investigative reaction may also be related to carrying pair behavior. In order to carry the male during copulation, the female's wings must dry before mating occurs. Thus, the evolution of the wing fluttering movement as a stimulus to the male in courtship may also have evolved in response to the hardening of the female's wings signaling her readiness to mate.

Results of the field experiments on *H. phylaeus* suggest that in the next phases of the courtship sequence, where the male follows the female and settles near her, virgin females are considerably more attractive to males than are already mated females or other males. Firstly, there was no observable difference in length of the following reaction between tethered male or mated female *phylaeus*; secondly, all of the successful matings observed were with virgin females; thirdly, the unsuccessful courtships with virgin females were longer and more involved than those with mated females. Color would thus not appear to play a major role in eliciting the following response of males. It may instead be that a pheromone emitted by virgin females attracts males after the investigative approach. Scott (1973a,b; 1974a) found evidence that virgin females of *Neominois ridingsii*, *Hesperia pahaska*, *Ochlodes snowi*, and *Lycaena arota* may possess a pheromone that attracts males at close range (within about a meter). *H. pahaska* and *O. snowi* are fairly closely related to *H. phylaeus*, being in the same tribe.

In later stages of courtship in *H. phylaeus*, odor again may be the primary stimulus eliciting the male's responses, especially in head-wing behavior, in which the male's head is thrust between the female's hindwings, touching her genital region. Tactile stimuli may also be functioning. In these later stages, species-specific pheromones would be adaptive to insure against hybridization with other species.

The stigma or pouch on the forewing of males of various butterfly species has been proposed to carry a pheromone which stimulates the female during courtship (Scott, 1973b; MacNeill, 1964). In *H. phylaeus*, the fluttering behavior of the male may



Fig. 3.—Curving Behavior of *Hylephila phylaeus* During Courtship Sequence (Male Genitalia are Extruded).

serve to disperse the pheromone from the stigma. Males often moved laterally to and in front of the female while fluttering their wings, thus possibly surrounding the female with scent. Similar results have been observed by Scott (1973a,b; 1974a) in *Amblyscirtes simius*, *Hesperia pahaska*, *Ochlodes snowi*, and *Lycaena arota*.

The rejection display by females may function in minimizing energy expenditure. When a rejection display abruptly halts a male's advances, wasteful energy expenditure is reduced—the female's energy can then be directed towards oviposition. A rejection display is thus advantageous only if it stimulates the male to abruptly terminate a futile courtship, as was the case in *H. phylaeus*. As a consequence, wasteful energy expenditure on the part of the male is reduced. Also, in attempting to court a previously mated female, a male's chances of successfully contributing to the next generation are decreased (assuming that sperm precedence occurs, Taylor (1967)), simply because such a female is older and has a shorter survival time during which to oviposit than does a newly emerged virgin. However, if virgin females are in short supply, any male's fitness is likely to increase if he attempts to mate any female he encounters. This is likely to be the case in species like *H. phylaeus* in which the average female mates only once but males may mate multiply, so the frequency of unsuccessful courtships involving non-virgin females observed in the wild is not surprising.

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VARIABILITY OF COURTSHIP OF THE BUCKEYE BUTTERFLY, *PRECIS COENIA* (NYMPHALIDAE)

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COURTSHIP BEHAVIOR OF BUTTERFLIES ranges from extremely stereotyped response in some species, to variability in other species (Scott, 1973). I have found that *P. coenia* has perhaps the most variable courtship of any butterfly studied to date. Mating of *P. coenia* was studied at Point Richmond, Contra Costa County, California, in connection with mark-recapture experiments (Scott, 1975), mainly by observing natural courtships and by releasing females in front of resting males.

Mate-locating behavior. *P. coenia* is a perching species as defined by Scott (1974a). Males perch primarily on bare spots of ground on fairly flat areas such as roadcuts and trails on hillsides, valley bottoms, and vacant fields. The larval foodplant (*Plantago lanceolata*) is most common in such sites, and females are most common near the foodplant. Males perch all day, especially from 0800 to 1400 (24-hour standard time). After 1400 fewer males show perching behavior, but some individuals still perch until 1600. Courtship and mating occur at the same time as male perching. 112 courtships and 27 copulating pairs occurred from 0815 to 1540, especially during the warmest part of the day. Virgin females were found at all times of day, and adults emerge from pupae in morning, indicating that some females wait until the day after emergence to mate. Females mate predominantly at the larval feeding sites, where males usually perch.

On cloudy or cold days few males perch and few courtships occur, but at temperatures of about 14-18°C individuals are able to perform most activities by basking (spreading the wings, moving the forewings forward, and orienting with the wings nearly perpendicular to the sun). Heinrich (1973) shows that

basking raises body temperature, and Blest (1975) showed that it may also reduce predation by displaying the eyespots which can startle predators.

Perching males sit on the ground and wait for a passing object. When an object appears, the male approaches near. Males investigate objects of a very wide size range. Three individual males followed for as long as possible investigated the following objects over a combined time span of two hours: a car (1 investigation); motorcycle (1); birds (11); a black and yellow butterfly (*Papilio zelicaon* Lucas) with 5 cm wingspan (2); an orange butterfly (*Colias eurytheme* Boisduval) with 4 cm wingspan (1); white butterfly (*Pieris rapae* L.) with 3 cm wingspan (2); other *Precis coenia* (32); a brown 2 cm wingspan butterfly (*Phyciodes campestris* Behr) (2); a white 2 cm wingspan butterfly (*Coenonympha tullia* Muller) (29); small grasshopper (1); small moths (2); small dragonflies (3); small bees and wasps (7); flies (5). These males sometimes investigated movement of vegetation due to wind, and made other investigative flights toward objects which I did not observe.

If the passing object is not another male or female *P. coenia* (of different appearance), the male usually returns to or near the previous spot. If a male chases another male which is flying past, the other male usually flies away when the perching male gets within 10 cm, and the perching male returns to the vicinity of his starting point. If two males which perch near each other investigate each other, they may separate or both may rise high in the air near each other then separate and descend to near the starting points, unless the encounter carries them too far away. Objects flying slowly (such as teneral males) seem to be pursued farther than erratically flying or swift objects, apparently because of greater resemblance to females. If a female passes by, the male pursues her for several meters until she lands, and courtship begins. Occasionally movement alone may be sufficient to attract the male for mating; one deformed female which could only hop erratically on the ground was found to be mated. Some females, especially older ones, are not pursued at all. If two males chase laterally more than ten meters from their previous sites, they seldom return. The males that were watched for up to several hours gradually moved over roughly a 30x30 m area, until they disappeared, usually because they pursued a female or another object for 20 m or more and did not return.

Courtship. Three stereotyped male and one female behavior patterns can occur in successful courtship: 1) *male hovering* consists of the male hovering in air by beating his wings at small amplitude, usually downwind just above the female; 2) *male fluttering* appears similar to male hovering but the male is on the ground behind the female, and the wings are usually moved with greater amplitude and lower frequency; 3) *male nudging* consists of the male, with his wings slightly raised and antennae pointing backward, pushing his head underneath the hind wings of the female (which are usually spread also) until his head is near her abdomen; 4) *female flapping* consists of the female on the ground flapping her wings at wide amplitude, continuously or in bursts (females flick their wings only occasionally when crawling during other activities).

Table 1 shows the association of these behavioral elements. In the simplest form of courtship, the female lands, raises her wings, the male lands behind, he moves alongside and bends his abdomen laterally (either right or left) to copulate. In a complicated courtship, after landing the female kept her wings spread, the male hovered then landed, the female flapped her wings and the male fluttered his, the male moved forward and nudged her, she raised her wings, he moved beside her and bent his abdomen to copulate.

Temporal patterns during courtship. Male hovering is most frequently observed just after the female lands either for the first time or after her short flights during courtship. The male then lands, whereupon male fluttering may occur. Male nudging generally occurs just prior to joining. Female flapping may occur whenever the male is on the ground just behind her. Virgins which are not very receptive often crawl or fly a short distance after being nudged. During courtship the female and male are sometimes quiescent, and movement by the female often leads to male nudging and abdominal bending.

Function of behavioral elements. Three behavioral responses during courtship seem to function similarly to the same responses in courtship of another Nymphaline butterfly, *Poladryas minuta* (Scott, 1974b). *Male hovering* and *male fluttering* are somewhat ritualized, but apparently help induce moderately unreceptive females to mate. *Male nudging* seems to function often merely as a technique for creeping under her wings if they are spread to enable the male to join; it may occasionally stimulate her to raise her wings to facilitate joining, and may also stimu-

late her to lower her abdomen so that joining may occur. Receptive females often raise their wings vertically and unreceptive females usually keep their wings spread. In one case the male nudged the female while her wings were raised. If the female does not lower her abdomen to slightly below horizontal or if she raises it slightly above horizontal, the male cannot grasp her. *Female flapping* is the "rejection dance" used to deter males. The females in Table 1 which copulated usually did not flap their wings or fly, but if they did, they flapped or flew weakly for a short time. Unreceptive virgin females flapped or flew less than did unreceptive mated females. When already mated females are pursued by males, the female generally flaps her wings vigorously upon landing, which seems to inhibit male responses somewhat (Table 1); then he usually flies away. The male may hover over the female for a moment. Female flapping resembles male fluttering closely, so may possibly cause the male to leave by convincing him that he is courting another male. Further evidence of this includes several observations in which a male chased another male, both landed on the ground and fluttered, then both flew away, and observations of teneral males flapping their wings when courted by another male. Females have other rejection behavior: 1) rarely an unreceptive female eluded a male by flying erratically. 2) an unreceptive virgin or newly mated female crawls or flies when the male tries to nudge or join; 3) she may raise her abdomen slightly so that he cannot copulate; 4) she keeps her wings spread, so that the male cannot crawl alongside to join and he must resort to "nudging." Courtship usually terminates unsuccessfully when the male departs. Sometimes, when hovering or crawling behind the female, he gets too far away and cannot relocate the female.

Role of vision and odor in courtship. Movement is necessary to elicit an investigative response by the male. By coloring all or part of a female's wings, I found that the general but not the detailed color pattern of the female is important in courtship. Virgin females with the upperside made completely black or red were usually ignored by males after a brief investigation, even though these females were courted for several minutes by other males before the females were colored. Females with several ocelli, white areas, or wings altered mated readily, however: one with the white areas on the forewings made black; one with the hindwing ocelli made green; one with the

ocelli of the left wings torn off. One female with crippled wings, and another less than half the normal size, had both mated. Males which had the dorsal wing surfaces blackened moved and apparently courted females normally (no copulations resulted because the females had already mated). One would expect the color and pattern of the male to be relatively unimportant because the male is behind the female during courtship.

The female might possess a pheromone. The shortest successful courtships involve nearly motionless females, which may indicate use of a pheromone for recognition. The most interesting observations concern interactions in which two males courted the same female; in three instances after one male joined, the other male continued attempts to join with the female, but did not attempt to join with the male of identical appearance. These males might have been able to recognize the female by following her movements during the interaction, or they might have used olfactory cues given off by one or both sexes.

Behavior during and after copulation. Immediately after joining, the male turns and faces opposite the female. Copulation lasts an average of 27 minutes (14-59, $S = 11.5$, $N = 14$). The female is more active than the male during copulation; she usually spreads her wings to bask, but the males does so only in about 30% of the copulating pairs. When disturbed, it is the female which carries the dangling male in flight; of 12 copulating pairs that were stimulated to fly, females flew 22 times, males never flew (some copulating pairs flew more than once). Copulation ends by the female crawling away dragging the male, and the female kicks with the hind legs and may turn until the male is broken off. The male then flies and the female remains for a short time.

Duration of courtship. Successful courtship lasted from only ten seconds when all wing movements and male nudging were eliminated, to 10 minutes 20 seconds. Unsuccessful courtship with virgin females lasted from 30 seconds to 20 minutes (often), rarely up to 9 minutes. Courtships with unreceptive mated females almost always lasted less than a minute.

Number of matings. Males probably can mate many times since they perch and mate at all ages, but only one male is known to have mated twice. Number of female matings was determined by counting spermatophores. Females predominant-

ly mate once, but occasionally mate twice and rarely three times (Table 2).

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Table 1.—Association of some of the behavioral elements of courtship: successful courtship of virgin females (left of the three positions separated by two dashes); unsuccessful courtship of virgin (middle) and mated (right) females. Terms are defined in text. Flying refers to a female flying during courtship.

Male	Female				Totals
	flapping, flying	flapping	flying	neither	
hover, flutter, nudge	-2-	-2-	- -	- -	-4-
hover, flutter	- -1	-2-	-1-	- -1	-3-2
hover, nudge	-3-1	1-2-1	-1-	1-1-	2-7-2
flutter, nudge	- -	2-1-1	-1-	-1-	2-3-1
hover	-3-3	1-5-3	-2-1	-5-	1-15-7
flutter	- -	-1-2	2-1-	2-1-	4-3-2
nudge	- -1	-4-1	- -	1- -	1-4-2
neither	-1-	1-3-15	1- -1	2- -	4-4-16
Totals	-9-6	5-20-23	3-6-2	6-8-1	14-43-32

Table 2.—Relationship between number of matings and apparent age (wing condition) of wild caught females. Totals are larger than sum of females rated once or twice because some females were not graded for wing condition.

		Wing Condition					
		Young				Old	Total
	0	38	0	0	0	0	38
Number of	1	23	9	12	11	7	95
Spermatophores	2	1	2	5	5	3	17
	3	0	0	0	0	1	1

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VARIATION IN *COLIAS ALEXANDRA CHRISTINA* EDWARDS

(PIERIDAE) IN SOUTHWEST MANITOBA

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MANITOBA LEPIDOPTERISTS HAVE TRADITIONALLY referred Manitoba populations of *Colias alexandra* Edwards to the subspecies *mayi* Chermock & Chermock; incorrectly however as *mayi* actually refers to *Colias gigantea* Strecker (e.g. Masters, 1971a), although they were assigned to *Colias christina* (now considered to be a subspecies of *alexandra*) by Chermock & Chermock (1940). The assignment of *mayi* to *gigantea*, ostensibly left the Manitoba population of *Colias alexandra* without a subspecific name which, in turn, led me to a series of studies which have culminated in this paper. In the course of this study I determined, to my complete satisfaction, that the Manitoba population of *Colias alexandra* is best referred to *Colias alexandra christina* Edwards of which *Colias eurytheme alberta* Bowman is a synonym (Masters, 1971b). This paper reports on the variability of *Colias alexandra christina* that is displayed in Manitoba populations.

SUBSPECIATION IN *COLIAS ALEXANDRA*

Colias christina (fig. 1) is the northern, predominately orange colored population of *Colias alexandra*. The orange *christina* phenotype occurs in the Great Slave Lake Region of the District of Mackenzie; south to Lake Athabasca and the Peace River Region of Alberta; thence eastward through northern Saskatchewan to the vicinity of The Pas, Manitoba; then southward along the Manitoba Escarpment to Riding Mountain and the vicinity of Brandon; and then appears again as an isolated population in the Black Hills of South Dakota (*krauthi* Klots). In southern Alberta and British Columbia, a broad band of gradual intergradation to the yellow phenotype (*alexandra*) begins. This intergradation zone continues through Montana,

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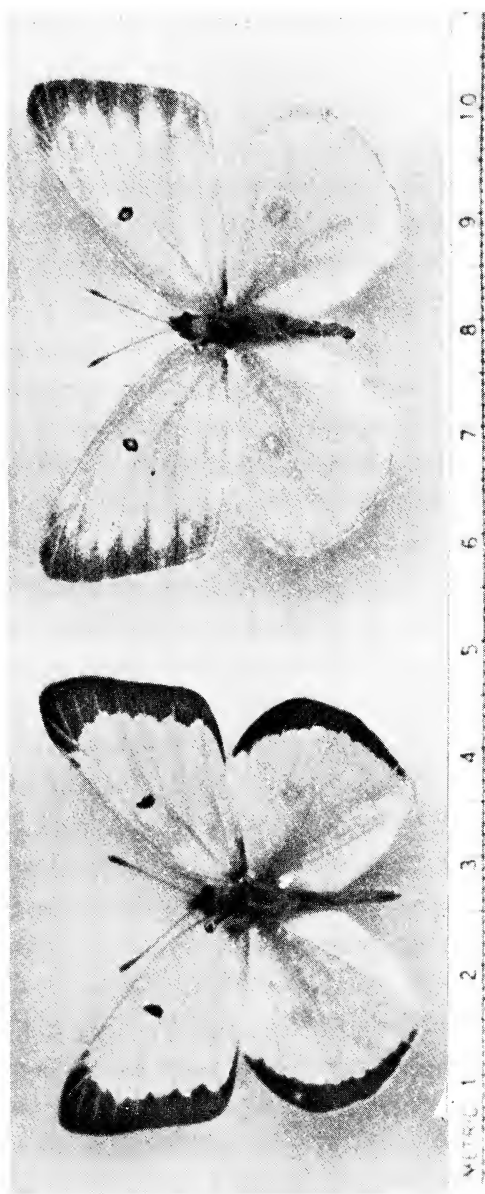


Fig. 1.—*Colias alexandra christina* Edwards. Birtle, Manitoba. Leg.: Jack Dennis. Male left, female right. Natural Size.

Idaho and northern Wyoming until typical *alexandra* is encountered in southern Wyoming and Colorado. The typical *alexandra* phenotype is found from Colorado; west into Utah; south into the White Mountains of Arizona and Sango de Cristo Range of New Mexico; and with an isolated offshoot in the Pine Ridge of Nebraska. The West Coast populations, are of a distinct albeit yellow phenotype. They range from the foothills in Southern California northward, west of the Sierra Nevada Divide and principally in foothills, to southern British Columbia. They are known as *harfordi* and *barbara* in the south and *occidentalis* and *chrysomelas* in the north. Hovanitz (1950) first allied all of these populations into one species, although this is still not universally accepted.

The name *astraea* Edwards is available to apply to the *alexandra/christina* blend zone population as a whole. Even though central Alberta specimens are quite distinct from northwest Wyoming ones, they are parts of the same cline.

MANITOBA POPULATIONS

In 1967, John Sorensen and I were of the opinion that Manitoba populations of *Colias alexandra* represented an undescribed subspecies. We were working on the mistaken premise that typical *christina* was represented by Southern Alberta populations as exemplified by specimens taken near Calgary. This is the same mistaken premise that many others (including Bowman, 1942) have made in dealing with *Colias christina*. Later comparisons of Manitoba *christina* with Edwards types of *christina* (at Carnegie Museum), other topotypical *christina*, Bowman's (1942) description and paratypes of *alberta* have convinced me that there are only statistical distinctions between them—and certainly not enough to warrant more than one subspecific name. Southern Alberta "*christina*" as well as populations from the Alberta Rockies are distinct, however, and they are, statistically at least, distinct from typical *astraea* from Wyoming; they are, as I have previously stated, part of the same cline (between *alexandra* and *christina*) as *astraea* and the names *christina* or *alberta* in the strict sense cannot apply to them at all.

I recently had the opportunity to examine and classify the collection of Lepidoptera, now in the Manitoba Museum of Man and Nature, assembled by Jack Dennis at Birtle, Manitoba between 1898 and 1944. Of considerable interest in this collec-

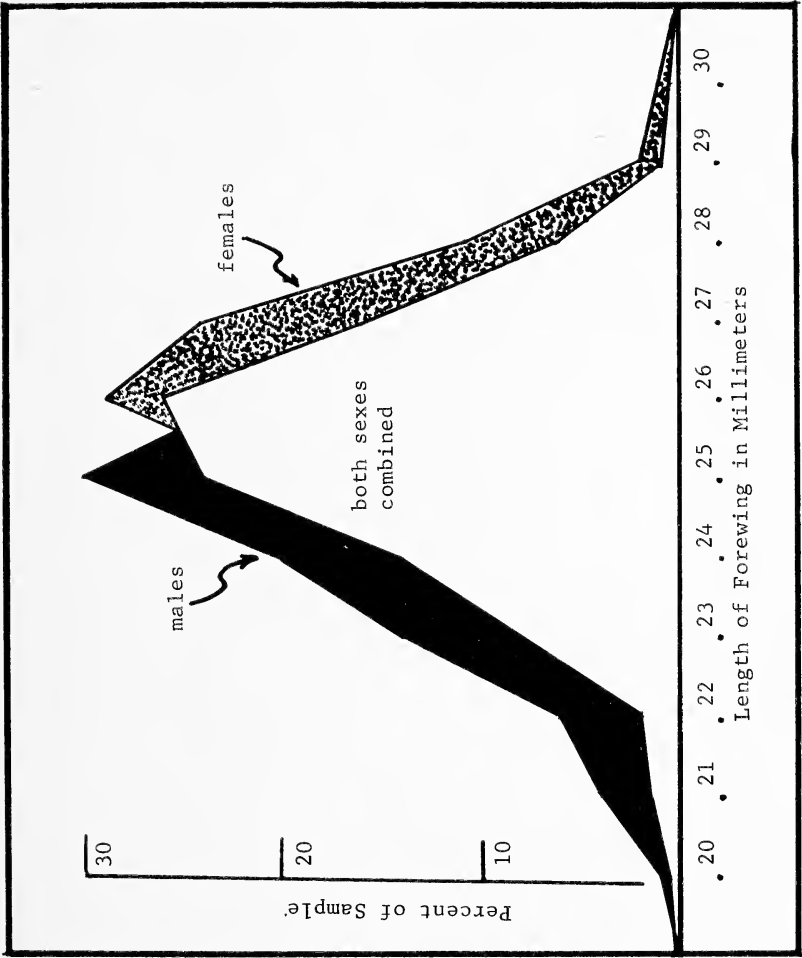


Fig. 2.—Distribution in size of 400 specimens of *Colias alexandra christina* from Birtle, Manitoba.

tion is a long series of *Colias alexandra christina*, containing over 400 specimens taken at Birtle over a 40 year span. Dennis was evidently very fond of *Colias christina* and dutifully filled at least one Riker Mount with 12 to 18 specimens of this species for each year he collected. This large collection, including specimens collected all season long for a lengthy period of time, provided an excellent opportunity to examine variation in this species at one given locality.

SIZE OF BUTTERFLIES. The first variable considered was the size of specimens, this was determined by measuring the length of the forewing to the nearest millimeter. The distribution in size for both sexes fall into typical bell-shaped curves (figure 2.). The median forewing length for males is 25 mm. and for females 26 mm., the average size for males slightly less than 25 mm. and for females slightly more than 26 mm. A series of 36 males and 36 females of toptotypical northern Alberta *Colias christina* (at Carnegie Museum) displayed slightly smaller size. Alberta males had a median forewing length of 24 mm., with the average slightly more than 24 mm.; the range was between 22 and 27 mm. Alberta females had a median forewing length of 26 mm., with the average being slightly less than 26 mm.; the range was between 19 and 29 mm.

FLIGHT PERIOD. Dennis' capture dates were interpolated to determine the flight period at Birtle (figure 3.). The male flight period is between June 12th and July 5th with a peak between June 16th and 23rd when the females are beginning to emerge. The female flight period is somewhat later, occurring between June 16th and July 14th and peaking between June 26th and July 2nd. The lack of Dennis specimens between July 4th and 6th is probably the result of some other activity that Dennis was engaged in that prevented his from field collecting at this time (perhaps he always used the week following Dominion Day to cut hay) rather than by an absence of individual butterflies at this time. There is a complete lack of individuals with collection dates during this time period throughout the Dennis collection.

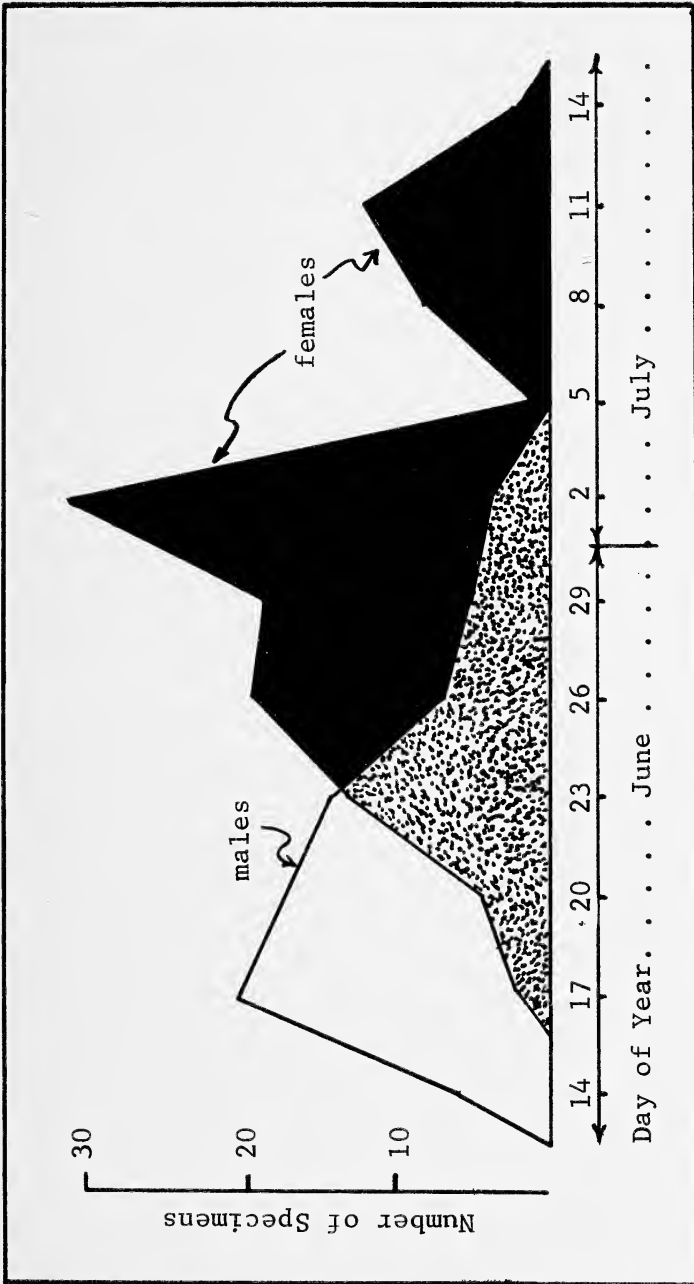


Fig. 3.—Flight period of *Colias alexandra christina* at Birtle, Manitoba as indicated by date of capture of specimens from the Dennis collection.

PHENOTYPE VARIATION. *Colias alexandra christina* is remarkable in that the males are extremely regular in appearance while the females are extremely variable. Males are always bright orange, with a basal yellow area, and have uniform black borders. Females may have an orange, yellow or white ground color and the black bands may be absent entirely or complete.

GROUND COLOR OF WINGS. 100% of the males examined had a uniform orange ground color to their wings. Of the females 68.1% were orange, 24.6% were yellow and 6.4% were white. Of the Alberta sample of nominate *christina*, only 27.8% of 36 females were orange, while 30.6% were yellow and 41.8% were white. The variation in the percentage of white females in *Colias* populations has been covered in detail by Hovanitz (1950b); he recorded 9.95% white females in Manitoba *Colias alexandra* and from 33.33 to 81.25% white females in various parts of Alberta. The relative lack of white females in the Manitoba population is unimportant from a subspeciation standpoint. The percentage of white females shows a great deal of geographical variation in all species of North American *Colias*.

BLACK BANDS OF WINGS. Males of *Colias alexandra* from localities throughout their range, display consistent black bands as in figure 1. Females, however, are quite variable showing a range from immaculate, to apex band on forewing, to outer band only, to complete band (see figure 4.). By judgement, although the distinctions are not discreet, each of 220 Birtle females was placed into one of the four categories with the following results: 1.8% showed immaculate wings, 14.5% had an apex band only, 22.8% had an outer band only and 60.9% had full bands. By comparison, the Alberta sample of 36 females contained 19.4% with immaculate wings, 44.4% with apex bands only, 22.2% with outer bands only and only 13.9% with complete bands. The bands of Alberta males are identical to the bands of Manitoba males.

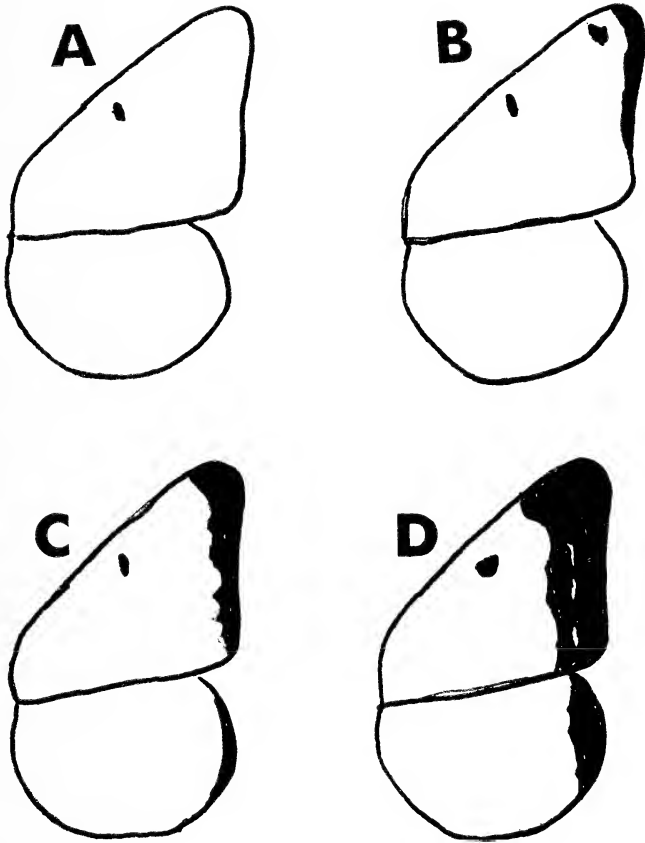


Fig. 4.—Variation in the dorsal black band patterns of female *Colias alexandra christina*. A. -immaculate wings. B. -band at forewing apex only. C. -outer band only. D. -complete band.

Condition of Black Band on Dorsal forewing	Ground Color of Wings			<u>TOTAL</u>
	<u>white</u>	<u>yellow</u>	<u>orange</u>	
<u>immaculate</u>	-	1.8%	-	1.8%
<u>apex only</u>	-	6.4%	8.2%	14.5%
<u>outer band</u>	0.9%	6.4%	15.4%	22.8%
<u>full band</u>	5.4%	10.0%	44.5%	60.9%
<u>TOTAL</u>	6.4%	24.6%	68.1%	100.0%

Fig. 5.—Table showing the co-ordinated abundance of the variation in the background color of the wings and the extent of black maculation of 220 females of *Colias alexandra christina* collected at Birtle, Manitoba.

CO-ORDINATED DISTRIBUTION OF BACKGROUND COLOR AND BLACK BANDS. The segregates of wing ground color and black band condition were platted against each other (figure 5.) to determine if there was any correlation between the two. Apparently there isn't and the genetic conditions that influence the black bands are independent of those that influence ground color. Nearly half, 44.5% of the Manitoba population displayed an orange ground color and complete wing bands. The Alberta sample of 36 females is too small to plot when 12 variables are involved. The largest individual segregate included 7 specimens (19.4%) with a yellow ground color and with apex bands only.

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THE ROLE OF WATERCRESS, *NASTURTIUM OFFICINALE*

AS A HOST OF NATIVE AND INTRODUCED
PIERID BUTTERFLIES IN CALIFORNIA

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THE MUSTARD FAMILY, Cruciferae, has a very distinctive insect fauna. The chemical basis for host selection by Crucifer insects was demonstrated as early as 1911 by Verschaeffelt, and has more recently stimulated both physiological and ecological studies (e.g. Thorsteinson, 1953; Schoonhoven, 1967; Feeny, Paauwe, and Demong, 1970). Root and Tahvanainen (1969) pointed out that, because of their dependence on mustard oils as phagostimulants, multivoltine Crucifer insects may require a seasonal succession of host species in a given locality. Many Crucifers are short-lived annuals, and even many perennial species (such as members of the genus *Dentaria*) are seasonally ephemeral. In the northeastern United States wintercress, *Barbarea vulgaris* R. Br., forms a critical element in the seasonal succession because it is the only very common Crucifer which overwinters as a well-developed rosette; it is thus available to many insects when alternative hosts are not. In lowland California most Crucifers are vernal species which disappear during the long, hot, dry summer. On the floor of the Sacramento Valley the introduced multivoltine cabbage butterfly, *Pieris rapae* Linnaeus (Lepidoptera, Pieridae) and the harlequin stinkbug, *Murgantia histrionica* Hahn. (Hemiptera, Pentatomidae), are able to continue breeding through the summer on two introduced weedy, perennial Crucifers, *Lepidium latifolium* L. and *Brassica geniculata* (Desf.) J. Ball. (Shapiro, unpublished data). Over a wide elevational range in the Sierra Nevada introduced watercress, *Nasturtium officinale* R. Br. (= *Rorippa nasturtium-*

aquaticum Schinz. and Thell.) appears to have a distinctive ecological role as a host to both native and introduced Crucifer insects. This paper reports its impact on the seasonality and spatial distribution of two Pierid butterflies, *Pieris napi microstriata* J. A. Comstock and *P. rapae*.

BIOLOGY OF THE PLANT

Nasturtium officinale is a succulent, perennial aquatic weed, native to Europe. Unfortunately there appears to be no archeological evidence to date its introduction into California (Robbins, 1940). Major waves of weed introduction occurred in the Mission period (1769-1800) and the Gold Rush (1849-1860s). Watercress is widely naturalized in California, forming well-defined colonies in shaded, quiet, shallow, flowing water from near sea level (about 40 feet, Fair Oaks, Sacramento County) to at least 7000 feet (Nevada, Placer Counties) (fig. 1). The plant cannot tolerate prolonged desiccation and is thus mostly confined to permanent streams. It colonizes intermittent springs, seeps, or runoff channels, but behaves as an annual there and is generally stunted. In the lower part of its elevational range it may have two seasonal maxima of flowering, one in spring and another in late summer. At higher elevations the flowering period is in early- to midsummer. As the seeds ripen the tops die back and new growth begins from the base and sometimes from nodes on the creeping stems. The plant overwinters as rosettes, which commence rapid growth in late winter or very early spring. Unlike the native perennial Crucifer *Dentaria californica* Nutt. which often grows near it on the sides of canyons, *N. officinale* is green and available to insects for most of the warm season. In its lower elevational range in the foothills it is normally the *only* Crucifer which is green in summer.

HOST RELATIONS OF *PIERIS NAPI*

Pieris napi is a Holarctic species or species complex occurring naturally (not by human intervention) in most of the cooler and montane parts of Eurasia and North America. The subspecies *P. n. microstriata* is confined to riparian habitats, generally in canyons, on the east slope of the Coast Ranges and the west slope of the Sierra Nevada in California. It is characteristically spring-univoltine and monophenic, unlike the coastal fog-belt sub-



Fig. 1.—Habitat of watercress, *Nasturtium officinale*, in stream bed, Washington Creek, Nevada Co., California; male *Pieris napi* fly up and down the stream bed “patrolling” for newly-emerged females.

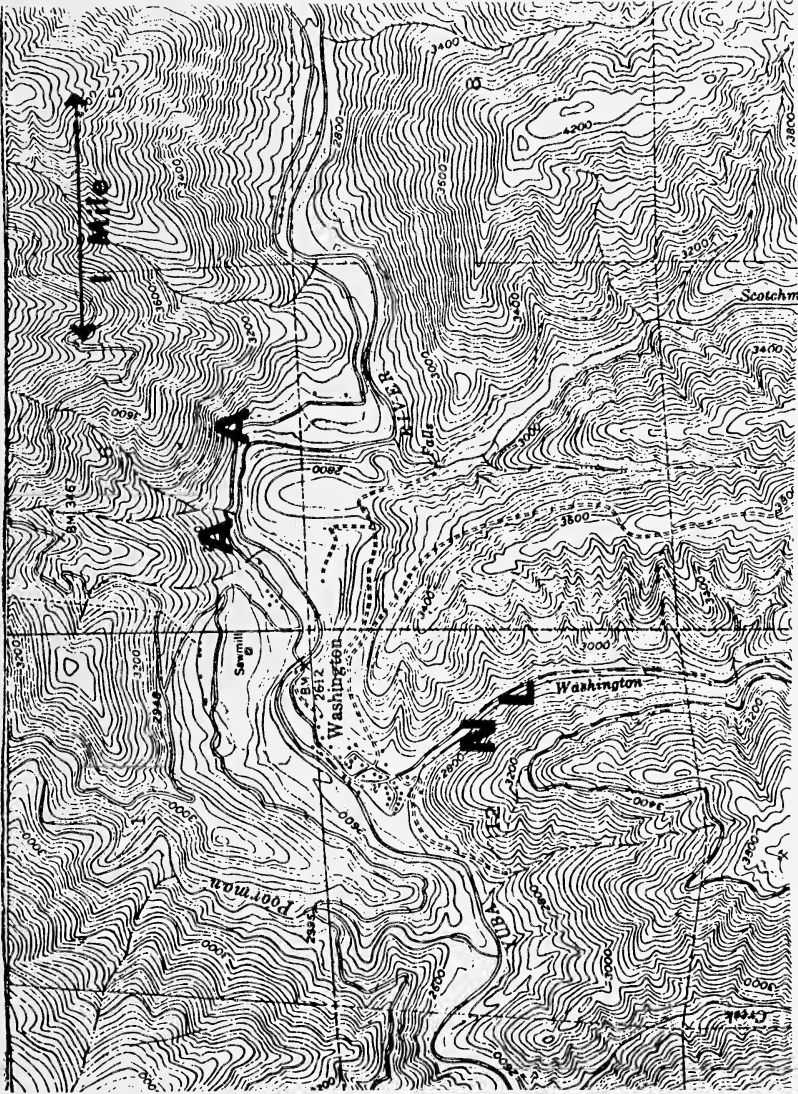


Fig. 2.—Spatial distribution of host records at Washington, Nevada County. A = *Arabis glabra*; N = *Nasturtium officinale*; L = *Lepidium virginicum* (see text).

species *venosa* Scudder (Shapiro, 1975a). In the literature its usual host association is *Dentaria californica*, whose vernal-ephemeral phenology generally fits that of the insect. Shapiro (1975b) reported *P. n. microstriata* breeding on *Arabis glabra* (L.) Bernh., a native annual, but not ovipositing on *Barbarea orthoceras* Ledeb., a native biennial, at Washington (2600 feet) and Lang Crossing (4500 feet) (both Nevada County); these are both spring plants. The development of local oviposition preferences seems to be routine for this animal. Thus at Baxter, Placer County (3900 feet) on 31 May 1975 three female *P. n. microstriata* were observed for about 20 minutes as they oviposited in a mixed stand of *Barbarea verna* (Mill.) Asch., *Lepidium campestre* (L.) R. Br., and *Arabis glabra*: eggs were laid only on the last. All three plant species were flowering and beginning to set fruit, and the females visited the blossoms of *B. verna* repeatedly. About 500 feet away many plants of *Lepidium virginicum* L. var. *pubescens* (Greene) Thell. (mostly not yet in flower) were growing in the road in much stronger sunshine, and they were not visited at all. (However, on 23 May 1975 several *P. napi* ova were found on this plant at Washington; see below.)

P. NAPI ON WATERCRESS

Given this selectivity, it is extremely striking that *P. n. microstriata* will apparently breed on *N. officinale* wherever the ranges of plant and insect coincide. The use of this plant was first called to my attention by R. L. Langston, who subsequently (1975) published it. Langston observed ovipositions on this plant near Placerville, El Dorado County (1850 feet). This locality was confirmed in 1975 and, more strikingly, *P. napi* was found breeding on watercress in close proximity to the localities where the host-selection observations reported in Shapiro, 1975b had been made. The spatial relationship between watercress and *Arabis* sites at Washington and Lang Crossing is shown in figures 2 and 3. Within the immediate vicinity of these sites the butterfly fails to utilize *Barbarea orthoceras* and *Lepidium campestre* although these plants are growing along *napi* "flyways" and may even be visited for nectar. *Lepidium virginicum* normally grows in quite different sites in full sun, but at Washington several plants were found in shade by the roadside a few feet from the stream bed where *P. napi* was breeding on watercress, and larvae were reared successfully to the adult from wild ova found on these plants.

At the altitude of Washington or Lang Crossing the phenology of *N. officinale* rather closely matches that of *Arabis glabra*,

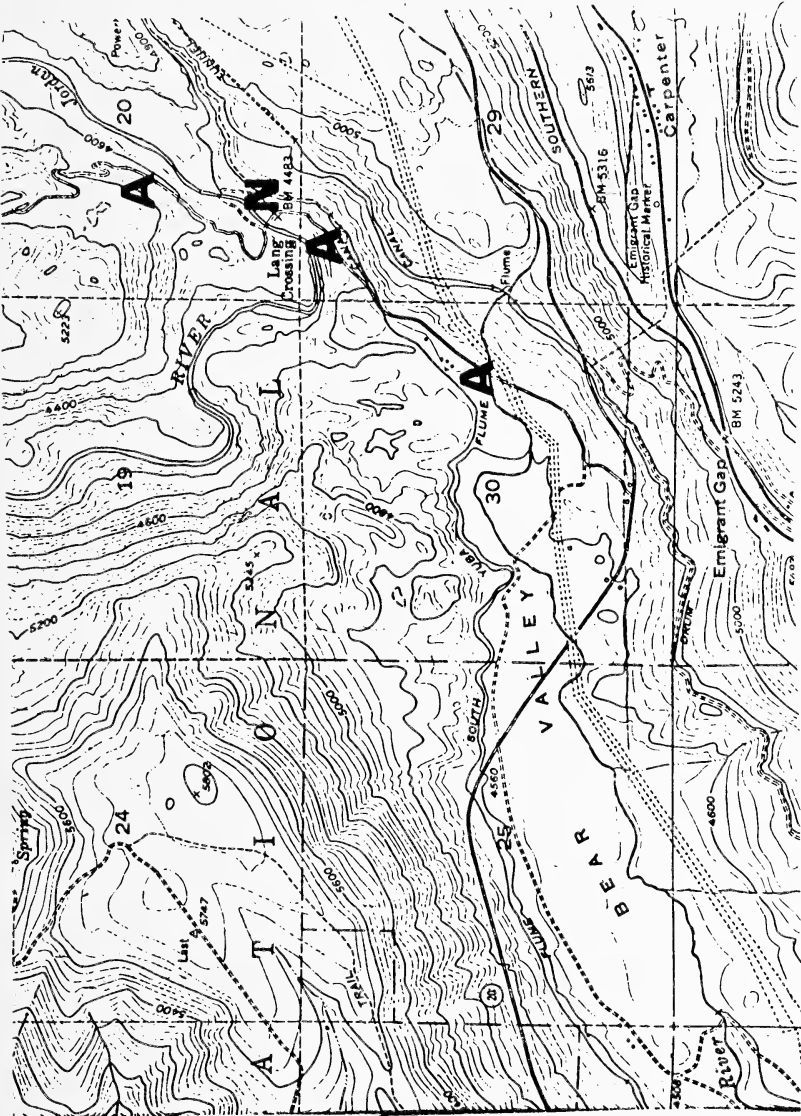


Fig. 3.—Spatial distribution of host records at Lang Crossing, Nevada County. Symbols as in figure 2 (see text).

and the seasonality of *P. napi* is unlikely to be altered by its presence. The butterfly is, however, undoubtedly able to maintain larger populations with than without it. Moreover, as it is perennial and occupies the same location from year to year, it provides a more reliable food source than does *A. glabra*, a successional species whose numbers may fluctuate widely from year to year. In this regard *N. officinale* resembles the native host *Dentaria*.

The situation is rather different in the foothills. Here the introduction of *N. officinale* may have allowed *P. napi* to expand both its range and its seasonality. The butterfly is common near Auburn in the American River gorge (Placer - El Dorado Counties, circa 650 feet) and is generally univoltine there as elsewhere in the Sierra Nevada, flying in early spring (March). In most of the gorge *N. officinale* is the *only* Crucifer. In two sites (fig. 4) *P. napi* is partially bivoltine in heavily shaded, cool, moist ravines where it breeds on lush growths of watercress. Although this bivoltinism appears to be due to microclimate rather than any genetic difference from adjacent univoltine populations (Shapiro, in preparation), neither uni- nor bivoltine *P. napi* could exist at all here in the absence of this introduced plant. Since California *P. napi* selects shaded ravine-riparian habitats, the preference of the plant for exactly these situations preadapted it as a host.

HOST RELATIONS OF *PIERIS RAPAE*

The European cabbage butterfly is generally considered to have entered North America in Quebec about 1860, but Reakirt's description of *Pieris yreka*, which appears to be this species, from California as 1867 suggests an earlier introduction there, possibly by the Spanish during the Mission period. *P. rapae* is now very widely distributed, from sea level to at least 8000 feet in disturbed habitats. It has a very long list of host records from lowland California (Shapiro, 1975c), but individual females tend to oviposit successively on the same Crucifer species, ignoring other potential hosts (unpublished notes). On the middle west slope of the Sierra its host preferences broadly overlap *P. napi*, including watercress and *Arabis glabra* but extending also to *Barbarea* and the two *Lepidium*s. Eggs and larvae of *P. rapae* have been collected from both watercress and *Arabis glabra* at both Washington and Lang Crossing, often from the

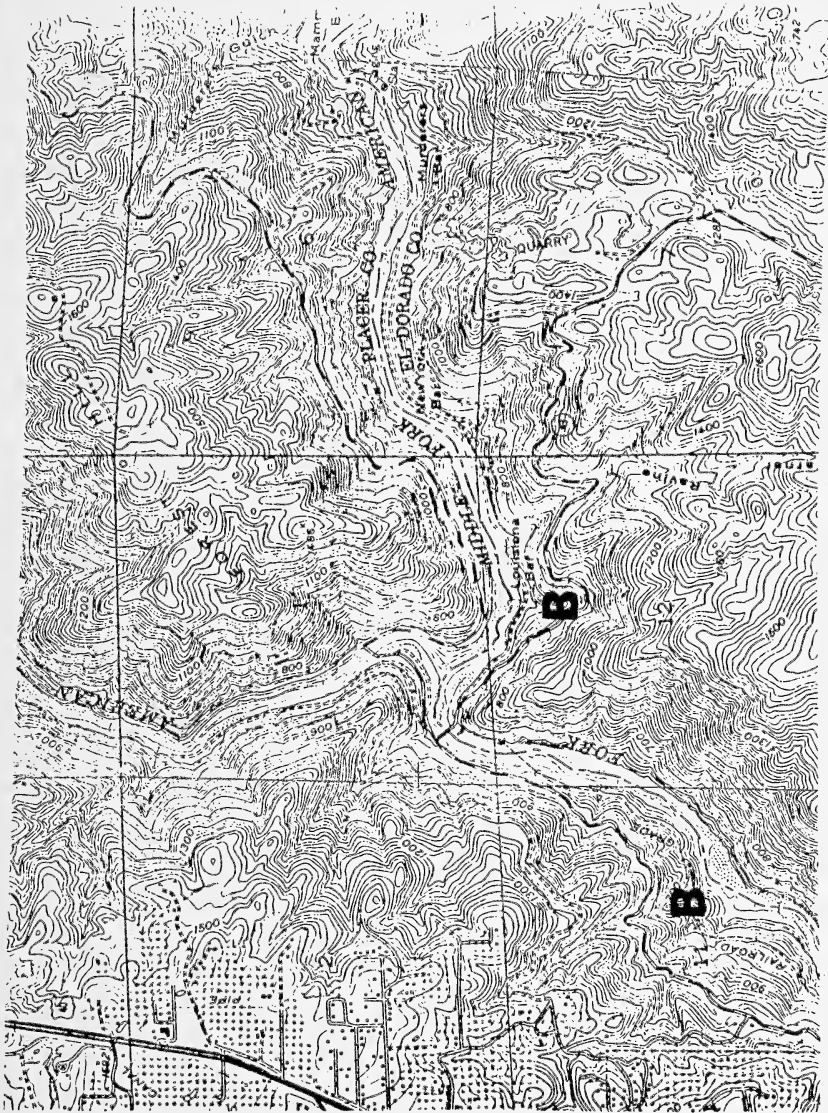


Fig. 4.—Locations of bivolvine *Nasturtium*-feeding populations of *Pieris napi* in the American River gorge near Auburn, California (see text).

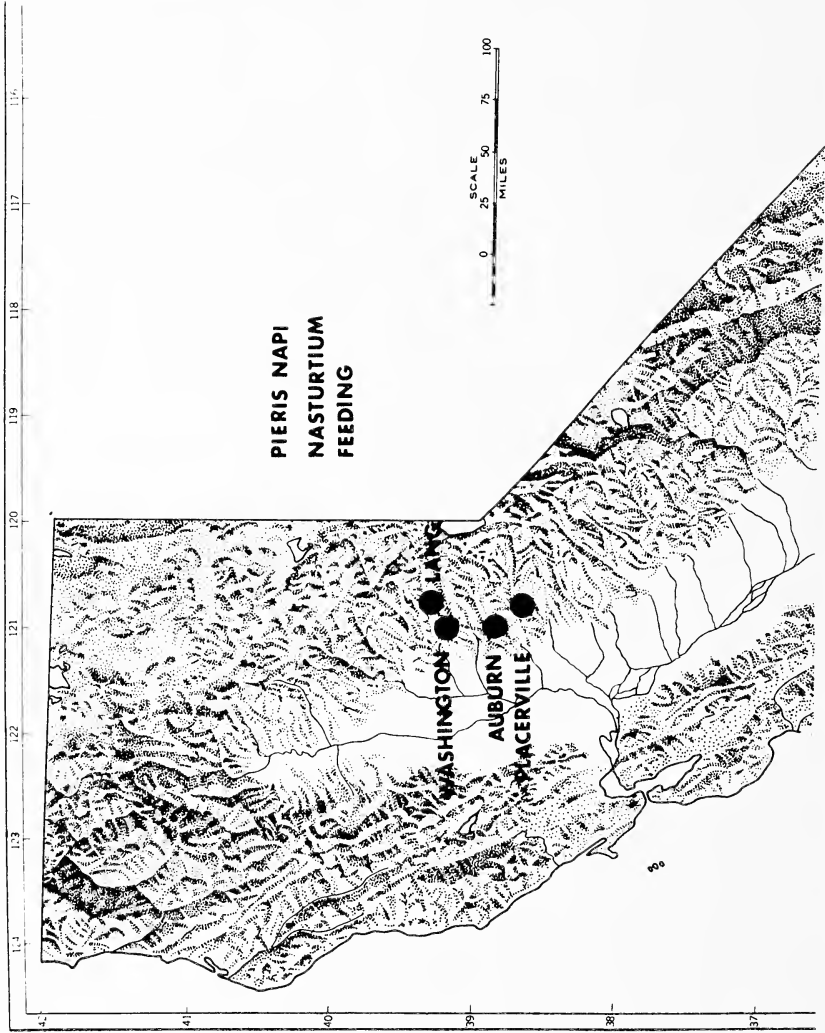


Fig. 5.—Localities where *P. napi* is known to feed on watercress in the Sierra Nevada. (Map from California Insect Survey, Univ. of Calif., Berkeley.)

same individual plants as eggs and larvae of *P. napi*. *Pieris rapae* is at least bivoltine at both stations.

In the American River gorge *P. rapae* (like *P. napi*) would be unable to exist in most sites in the absence of watercress. (It does breed along the arid roadside on scattered plants of *Brassica geniculata* growing in disturbed soil.) In one of the ravines where *P. napi* is bivoltine, an attempt was made on 1 July 1975 to collect second-generation *napi* larvae on watercress. Careful search of the entire stand produced only ten larvae of *P. rapae*, despite the fact that female *napi* had been flying there ten days earlier. Conditions at this site are much more mesic than on the roadside mustard in full sun, and wild *P. rapae* consistently prefers high water content Crucifers (such as *N. officinale*) over low water content species (*B. geniculata*) where a choice is available.

DISCUSSION

Lees and Archer (1974) group the hosts of *P. napi* in Britain according to field preference. They list watercress in group 1, i.e. plants on which females "were frequently and regularly observed to oviposit," and "from which larvae could readily be obtained by searching." There is no need to invoke genetic adaptation to a new host by Californian populations of *P. napi*; watercress seems to be intrinsically "desirable" as a *napi* host, and its utilization wherever it occurs on the Sierran west slope argues powerfully for this. It does have the potential disadvantage of liability to flash flooding, but this phenomenon was not actually observed at any Sierran locality under study in 1974 or 1975. Figure 5 summarizes the localities at which *P. napi* has been found breeding on watercress to date.

There is no native, aquatic, perennial Crucifer in the California flora. The native annual to biennial species *Rorippa curvisiliqua* (Hook.) Bessey has a wide elevational range, but grows in streams and seeps in meadow habitats, where Californian *P. napi* do not occur. (It is used by *P. rapae* at Donner Pass (7000 feet) (Shapiro, 1975d) but this butterfly has not been found on it in the Sacramento Valley. There, *R. curvisiliqua* is a spring species, very infrequent and inconspicuous compared to the rank, weedy "mustards.") The introduction of watercress, with its unique characteristics, permitted the expansion of the niches of the native butterfly *Pieris napi microstriata* and the introduced, weedy butterfly *P. rapae* in California. Its aquatic

perennial habit ideally preadapts it as a refuge for multivoltine species during the hot, dry lowland California summer and it may be expected to fill the same role for other members of the Crucifer fauna.

ACKNOWLEDGMENTS

I thank Mr. Robert L. Langston for calling watercress to my attention as a host of *P. napi*; Mr. William Patterson for showing me the American River localities for bivoltine *P. napi*; Dr. William Hovanitz for the photograph of Washington Creek (fig. 1); Dr. Frances Chew for stimulating discussion; and the Committee on Research of the Academic Senate, UCD, for its continuing support of our investigation of seasonality and colonizing ability in *Pieris*, through grant D-804.

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TABLE 1
PLANT FORMATIONS IN THE SIERRA DE TUXTLA

A. MONTANE FORMATIONS

- (1) Lower Montane Rain Forest (*Terminalia-Dalbergia* Association)
- (2) Montane Rain Forest or Cloud Forest (*Engelhardtia-Quercus* Association)
- (3) *Liquidambar-Quercus* Associes
- (4) Montane Thicket (*Podocarpus-Thouinidium* Association)
- (5) Elfin Woodland (*Quercus-Clusia-Podocarpus* Association)

B. SEASONAL FORMATIONS

- (6) Semi-Evergreen Seasonal Forest (*Bursera-Inga* Association)
- (7) *Bursera-Sabal-Orbignya* Associes

C. SEASONAL-SWAMP FORMATIONS

- (8) Savanna (*Curatella-Byrsonima* Association)
- (9) Deciduous Woodland (*Quercus* Consociation)
- (10) *Pinus-Quercus* Associes

D. DRY EVERGREEN FORMATION

- (11) Littoral Woodland or Dry Evergreen Woodland (*Ficus-Hibiscus* Association)

E. SWAMP FORMATIONS

- (12) Swamp Forest (*Pachira-Ficus* Association)
- (13) Mangrove Woodland (*Rhizophora* Consociation)

F. MISCELLANEOUS FORMATIONS

- (14) Recently Abandoned Milpas
- (15) Pastures
- (16) Hedgerows

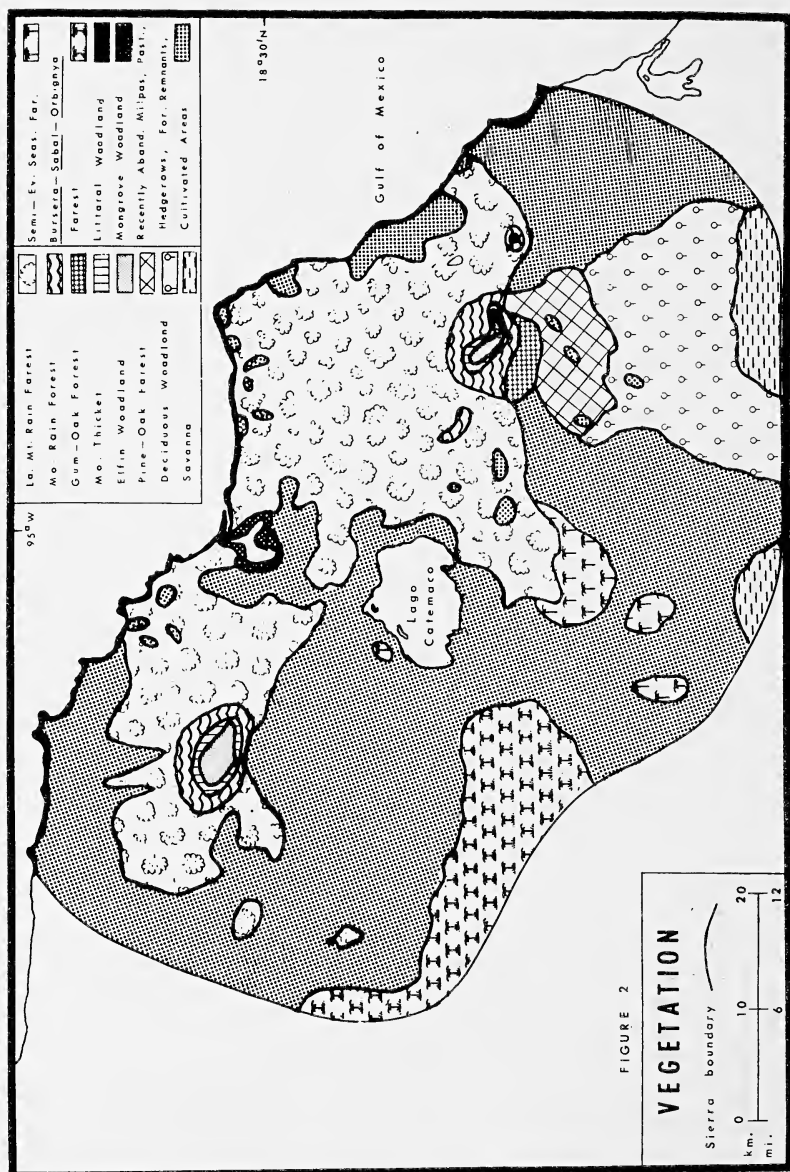


FIGURE 2
Vegetation of the Sierra de Tuxtla.

The analyses of the vegetation in the following discussion are based on samplings by both Andrle and myself. In no instance was an effort made to completely characterize a vegetative type. Usually only the apparently more common members that were either in blossom or fruit were collected. (All plant specimens were donated to the United States National Museum.) Throughout the discussion plant species are listed in descending frequency of abundance. Also, several terms belonging to the science of plant ecology are used, and in order to avoid confusion, are defined below.

1. Dominant—"those members of the community which exert a controlling influence over the other components" (Beard, 1944). These were chosen empirically according to size and abundance.

2. Association—"the largest possible group which has consistent dominants" (Beard, 1944). When possible I have tried to characterize the association with the generic names of the two most common dominants. However, in certain instances this limitation could not be imposed so three names had to be employed.

3. Consociation—"a group of equivalent rank to the association where there is only one clear dominant" (Beard, 1944).

4. Associates—the major unit of a sere (Clements, 1936), a sere being defined as "any community which is patently in a state of change, development or transition" (Beard, 1944).

MONTANE FORMATIONS

Although Andrle (1964) classified all of the relatively undisturbed and "tall forests" of the range in two categories—"Rain Forest" and "Cloud Forest"—he did recognize that the formations were not homogeneous throughout their extent. My investigations indicate that the diversification within each type is sufficiently pronounced to warrant the formations divisions into subcategories, which can be correlated with the various "Montane Formations" of Beard (1955).

1. Lower Montane Rain Forest (*Terminalia-Dalbergia* Association); Plate 5.

This formation encompasses the "Rain Forest" of Andrle (1964) and exists principally on the slopes of the major volcanoes. On the Gulf slopes the formation occurs within an altitudinal range of approximately 50 to 3,000 feet. The most extensive areas remaining south of the high long axis of the range



PLATE 5

Lower Montane Rain Forest near Vigía. May 1965, 1,700 feet.

are in the vicinity of Cerro Cintepec, the Curbres de Bastonal, and southwest of Volcán San Martín Tuxtla (Andrle, 1964).

Until five to seven years ago the forest on the Gulf slopes was relatively undisturbed by man. But since then there has been a rather steadily accelerating movement of people from the more densely populated leeward slopes around and onto the Gulf facing slopes. This in turn has resulted in forest destruction so that presently there exist rather extensive (but disjunct) areas that are already cleared or are in the process of being cleared. On the leeward slopes the forest is very much reduced because of several factors. First, because of extensive cultivation involving both corn and coffee, the former occurring in no restricted zone and the latter occurring principally in a zone between 2,300 and 2,900 feet in elevation; second, because of a relatively low annual precipitation due to a rain shadow effect; and third, because of unfavorable edaphic conditions, particularly on the Santa Marta massif.

Andrle (1964) stated that the "Rain Forest" seems to have its nearest affinities with the "Seasonal Evergreen Forest" of Beard (1944) because of the presence of an understory composed principally of palms and because several of the dominant trees exhibit buttressing. However, as indicated subsequently by Beard (1949), these two characteristics are also shared by the Lower Montane formation but that the critical factors that determine the Lower Montane formation are the presence of only two distinct tree strata and simple leaved dominants, both of which are characteristic of the forests at relatively low elevations in the Sierra. Furthermore, since the three formations that exist on the slopes at higher elevations correlate very well with other subdivisions in Beard's Montane sequence, I conclude that the forests between 50 and 3,000 feet should be considered a typical Lower Montane Rain Forest.

The flora within this formation is very rich. Ground vegetation is relatively sparse and includes *Aphelandra aurantiaca* and *Didymochlaena truncatula* (Andrle, 1964). Above this is a zone of saplings and shrubs, which include *Hamelia longipes*, *Myriocarpa longipes*, *Cephaelis elata* (Andrle, 1964), *Psychotria* sp., and *Deherainia smaragdina*. Because of the relative sparseness of ground vegetation, walking upright in the formation is not difficult.

The lowest tree stratum ranges between 10 and 18 feet and is composed predominantly of palms—*Astrocaryum mexicanum*



PLATE 6

Montane Rain Forest or Cloud Forest on Volcán Santa Marta. April 1965,
3,200 feet.

and *Chamaedorea tepejilote* being the most common. The dicot *Aegiphila costaricensis* is also very common.

A distinct middle stratum cannot be differentiated from an upper stratum of emergents. In most cases the tallest trees—*Terminalia amazonia*, *Dalbergia* sp. and *Bernoullia flammea*, *Talauma mexicana*, *Pithecollobium arboreum*, *Mirandaceltis monoica*, *Phoebe mexicana*, *Engelhardtia guatemalensis*, and *Virola guatemalensis* (Andrle, 1964)—although ranging from 90 to 110 feet in height, do not protrude significantly above the canopy to warrant the title of emergents. Thus it is best to combine them with the slightly lower species such as *Pseudolmedia oxyphyllaria*, *Stemmadenia galeottiana*, *Pleuranthodendron mexicana*, *Calatola* sp., *Clethra macrophylla*, *Saurauia* sp., *Annona* sp., *Coccolaba* sp. (Andrle, 1964), and *Rinorea guatemalensis* into a single upper stratum or canopy layer that ranges between 70 and 110 feet in height.

Lianas and the climbing fern *Dryopteris* sp. are common on the trunks of many trees. Epiphytes are relatively uncommon and occur principally in tree crowns.

Within this formation there appears to be a continual shedding of leaves by the component species although there is a heavier leaf fall near the end of the dry season (May). Only *Bernoullia flammea* was observed to lack leaves for any extended period during the dry season. Also, there appears to be no distinct flowering or fruiting season although flowering, like leaf fall, is more common towards the end of spring.

Where relatively substantial openings exist in the forest, e.g., along logging roads and trails, *Boeheria* sp. and *Urera elata* usually form dense thickets, which attain maximum heights of 8 to 12 feet.

2. Montane Rain Forest or Cloud Forest (*Engelhardtia-Quercus* Association); Plate 6.

This formation is located above the Lower Montane formation and ranges between approximately 3,000 and 4,100 feet on Volcáns San Martín Tuxtla and Santa Marta but to only 3,500 feet on Volcán San Martín Pajapan because of the latter's slightly lower elevation.

Ground vegetation is similar to that in the Lower Montane formation. Above the ground cover is a zone of saplings and shrubs of which the most common are *Cephaelis elata*, *Chamaedorea ernesti-augustii*, *Deppea excelsa*, *Rudgea cornifolia*, *Engelhardtia mexicana*, and *Ceratozamia mexicana*.



PLATE 7
Gum-oak forest on Volcán Santa Marta. May 1965, 2,700 feet.

Only two tree strata are present. The lower stratum ranges between 15 and 30 feet and includes *Eugenia* sp., *Chamaedorea elegans*, *Chamaedorea* sp., *Eupatorium tuerckheimii*, *Solanum schlechtendalianum*, and *Carpinus caroliniana*. Tree ferns, *Cyathea* sp. and *Alsophila schiedeana* (Andrle, 1964), are very common in the numerous ravines and ridge slopes.

The upper stratum ranges between 50 and 70 feet and includes *Engelhardtia mexicana*, *Quercus skinneri*, and *Rheedia edulis*.

Lianas and epiphytes are more common than in the Lower Montane formation; epiphytes are not restricted to tree boles. Trunks and limbs usually are festooned with mosses, algae, and ferns.

3. *Liquidambar-Quercus* Associes; Plate 7.

The gum-oak forest, which appears to be a subclimax community, is restricted to a narrow zone on the southern slopes of Volcán Santa Marta between elevations of 2,500 and 3,000 feet. However, both dominants occur sporadically in the Montane Rain Forest on Volcán San Martín Tuxtla and on small isolated hill slopes northeast and northwest of Lago Catemaco.

Ground vegetation is relatively sparse although there is a dense understory of shrubs, bushes, and saplings of which the most common are *Cephaelis elata*, *Siparuna andina*, *Phoebe bourgeauviana*, *Erythroxylon tabascense*, *Hirtella racemosa*, *Rinorea guatemalensis*, *Croton glabellus*, *Rondelitia galeottii*, *Persea longipes*, *Machaonia* sp., and *Casearia sylvestris*.

The understory forms a gradient up to the canopy layer that ranges between 30 and 50 feet in height and which consists primarily of *Liquidambar styraciflua*, *Quercus ghiesbrechtii*, *Belotia* sp., *Casearia nitida*, and *Alchornea latifolia*.

The gum trees usually drop their leaves in early February and remain leafless for approximately two to three weeks after which time new growth and blossoms appear. The oaks usually do not lose their leaves until late March or early April; new growth and blossoms appear immediately thereafter.

Andrle (1964) suggests that the gum-oak forest exists because of a combination of factors—destruction of the preexisting vegetation by man, lowered soil fertility from extensive weathering, and rainfall that is slightly lower than that in other sections of the Sierra because of the “broad, high front presented by the south crater walls of Cerro Campanario and Volcán Santa Marta.”



PLATE 8

Montane Thicket on Volcán Santa Marta. April 1965, 4,700 feet.

Although all three factors probably are operational, it is my opinion that the first two are of greater significance than the third. The Popoluca Indians have been intensively utilizing the area within the present-day gum-oak forest for the cultivation of their corn and coffee for hundreds of years since corn and coffee do not grow well in the pine and oak forests that surround the Indian villages. The corn fields are used only for three to five consecutive years; they then are abandoned and succession is allowed to proceed. Within 20 to 30 years a rather substantial forest of gum and oak becomes established. This is then cut and burned and hence the cycle is begun anew. Very few areas are allowed to proceed beyond the gum-oak community for arable land is at a premium. However, those few areas that remain uncut for longer periods develop a forest that gradually acquires the characteristics of the Montane Rain Forest that occurs presently slightly higher in elevation. Thus, I conclude that intensive agriculture with its inevitable lowering of soil fertility is the primary factor for the existence and maintenance of the *Liquidambar-Quercus* Associates in the Sierra and that this associate is a subclimax community in the Montane Rain Forest formation.

4. Montane Thicket (*Podocarpus-Thouinidium* Association); Plate 8.

This formation, which corresponds in part to the "Cloud Forest" of Andrieu (1964), occurs between approximately 4,100 and 4,800 feet on Volcáns San Martín Tuxtla and Santa Marta but is absent on Volcán San Martín Pajapan. In physiognomy the forest is slightly modified from that described by Beard (1949) inasmuch as there is a distinct and dense understory of shrubs and small trees in addition to the canopy layer. This understory ranges between approximately 15 and 30 feet in height and consists principally of *Clethra suaveolens*, *Oreopanax xalapense*, *Oreopanax capitatum*, *Xylosma* sp. (Andrieu, 1964), *Engelhardtia mexicana*, *Ardisia* sp. (?), *Thouinidium decandrum*, *Eugenia* sp., *Deppea excelsa*, and *Rudgea cornifolia*.

The canopy layer ranges between 45 and 60 feet in height and is composed principally of *Podocarpus oleifolius*, *Thouinidium decandrum*, and *Engelhardtia mexicana*.

Tree trunks (usually with no extensive buttressing) and branches support luxuriant growths of mosses, lycopodiums, ferns, bromeliads, and orchids (*Elleanthus capitatus* being a common species). Lianas aren't as common as in the Montane



PLATE 9

Elfin Woodland on peak of Volcán Santa Marta. April, 1965, 5,100 feet.

Rain Forest.

The forest on the crests of several of the steep ridges on Volcán Santa Marta has been cut by the Popolucan Indians in order to establish hunting trails up to the crater. In these relatively open areas there is a seral community in which the palms *Chamaedorea elegans*, *Chamaedorea ernesti-augustii*, and *Chamaedorea* sp. predominate and which tends to resemble the "Palm Break" subclimax community of Beard (1944; 1949). However, because of the restricted distribution of this community in the Sierra, I think that the community does not warrant the rank of formation.

This formation (and the succeeding one) frequently are enveloped in clouds caused by the condensation of moist air moving in on the north and northeast winds from the Gulf. Although mist is more prevalent during the rainy season, there are enough misty days during the dry season to maintain a relatively high constant humid condition.

5. Elfin Woodland (*Quercus-Clusia-Podocarpus* Association); Plate 9.

This formation is the highest in the Montane sequence and is limited to the upper ridges and crater rims and walls of the three principal volcanoes. The forest begins approximately at 4,800 feet on Volcáns San Martín Tuxtla and Santa Marta and at 3,400 feet on Volcán San Martín Pajapan. However, on ridges that are very steep and frequently exposed to strong winds (particularly on Volcán San Martín Pajapan and Cerro Tuxtla), elements of this formation occur at much lower elevations (as low as 2,700 feet). The numerous ravines within this formation contain elements of the Montane Thicket and/or Montane Rain Forest.

Ground vegetation is very luxuriant and consists of a thick mat of mosses and lichens that support profuse numbers of orchids and bromeliads. Where the canopy is relatively open and light penetration is good, grasses, principally *Aulonemia* sp. and *Isachne arundinacea*, the sedge *Rhynchospora tuerckheimii*, and numerous small bushes and shrubs such as *Miconia glaberrima*, *Centropogon affine*, and *Solanum* spp. are common. The fern *Gleichenia palmata* and the cactus *Agave* sp. are locally common, especially on open, exposed ridges.

There is but one tree stratum and this consists of a gnarled, interlaced, many branched, and almost impenetrable growth of small trees ranging between 8 and 20 feet in height and con-

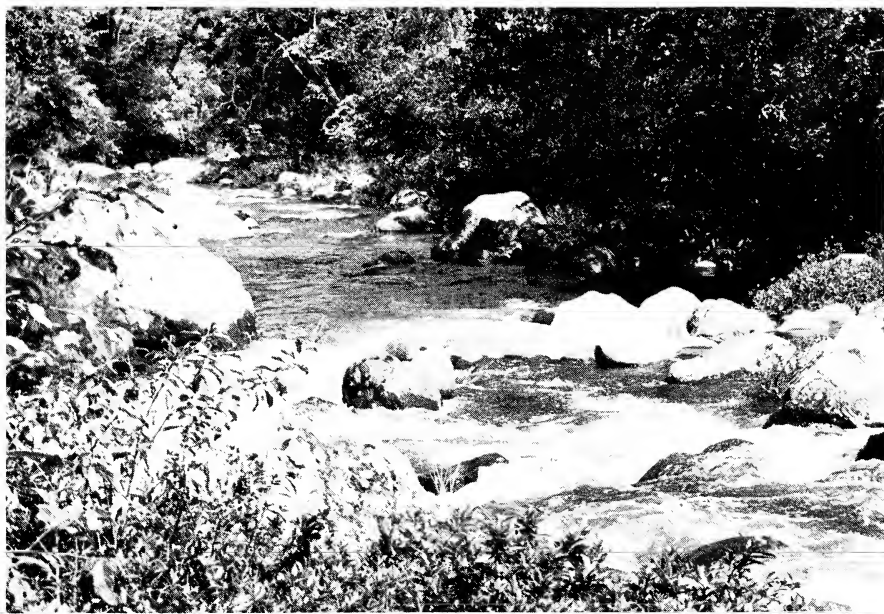


PLATE 10

Semi-Evergreen Seasonal Forest. TOP, forest near Barrosa. Area in foreground was cut and burned for corn cultivation. June 1962, 500 feet. Photograph from Andrie (1964) and used with the author's permission. BOTTOM, forest in ravine on Volcán Santa Marta near Ocotlán Chico. July 1965, 1,700 feet.

sisting of *Quercus ghiesbreghtii*, *Clusia salvinii*, *Podacarpus oleifolius*, *Albizia* sp., *Phoebe psychotrioides*, *Ardisia* sp. (?), *Weinmannia pinnata*, *Gaultheria* sp., *Myrica cerifera*, *Solanum* sp., *Ceiba pentandra*, and *Gymnanthes actinostemoides*. Andrle (1964) recorded the following additional species: *Senecio* sp., *Hoffmania lenticillata*, *Viburnum acutifolium*, *Ilex nitida*, *Oreopanax xalapense*, and *Clethra suaveolens*.

Practically every branch, limb, and trunk is profusely festooned with mosses, principally *Pterobryum densum* and *Pilotrichella flexilis* (Andrle, 1964), ferns, lycopodiums, bromeliads, and orchids, principally *Elleanthus capitatus*. Many of the top-most branches of the tallest trees are dead. Not all species are evergreen; *Albizia* sp. (?) remains leafless during the dry season. Flowering and fruiting of all species are most common during the spring dry season.

Landslides resulting from mild earth tremors occasionally occur along the steep walls of the three primary craters (particularly on Volcán Santa Marta). These slides create openings in the forest and produce optimal conditions for primary succession. One of the most common angiosperms to appear shortly after a slide is *Schistocarpha* sp.

As stated previously, this formation and the Montane Thicket frequently are enveloped in mist, a fact that tends to make insect collecting very difficult.

SEASONAL FORMATIONS

6. Semi-Evergreen Seasonal Forest (Bursera-Inga Association); Plate 10.

This formation corresponds to the "Semi-Deciduous Forest" of Andrle (1964). Because of man's agricultural practices, the forest exists today only as remnants, principally on ridges and slopes in the southern part of the range where annual precipitation is usually less than 70 inches (primarily south of Cerro Cintepec), in the vicinity of Lago Catemaco, and in the numerous ravines within the Deciduous Woodland (including the *Pinus-Quercus* Associes) on the Santa Marta massif.

Ground vegetation is scanty although there is a dense understory of saplings and herbaceous plants. Common species include *Piper* spp., *Odontonema callistachyum*, *Acalypha diversifolia*, *Myriocarpa bifurca*, and *Heliconia latispatha*. The palm *Orbignya* sp. occurs sporadically throughout the formation.

Two tree strata are present. The lower stratum ranges be-



PLATE 11

Bursera-Sabal-Orbignya Forest near Tibermal, August 1962, 200 feet. Photograph from Andrie (1964) and used with the author's permission.

tween 15 and 30 feet in height and is composed principally of *Cecropia mexicana*, *Acalypha diversifolia* var. *carpinifolia*, and *Tabernaemontana citrifolia*. Along streams *Erythrina mexicana* is common.

The upper stratum ranges between 40 and 60 feet in height and consists primarily of *Bursera simaruba*, *Inga spuria*, *Inga leptoloba*, *Luehea speciosa*, *Myrcia splendens*, *Albizia idiopoda*, *Dendropanax arboreus*, *Ilex belizensis*, and *Roupala borealis*.

Trees usually branch low and the boles frequently are umbrella-shaped. Buttressing is uncommon. Trunks usually support numerous lianas and vines (such as *Anguria tabascensis*). Epiphytes are relatively uncommon.

During the dry season several of the dominants drop their leaves and remain leafless until the onset of the summer rains. 7. *Bursera-Sabal-Orbignya* Associes; Plate 11.

In the extreme southwest section of the range and at slightly lower elevations than the Semi-Evergreen Seasonal Forest is found a community that appears to be of subclimax rank. This forest is composed principally of *Bursera simaruba* and the palms *Sabal* sp. and *Orbignya* sp. Other trees include *Cecropia mexicana*, *Inga spuria*, *Cassia spectabilis*, and *Cassia occidentalis*. There is no definite canopy since the trees usually exist in dense, disjunct stands separated by extensive tracts of coarse grasses, sedges, and herbaceous plants of which the most common are *Paspalum* spp., *Sporobolus* spp., *Rynchospora* spp., *Dichromena ciliata*, *Asclepias woodsoniana*, *Melanthera angustifolia*, and *Stemodia durantifolia*. These open areas seem to be the result of, and, to be perpetuated by repeated burnings by the local Mexicans and intensive pasturing by livestock.

SEASONAL-SWAMP FORMATIONS

8. Savanna (*Curatella-Byrsonima* Association); Plate 12.

This formation, which seems to correlate well with the Orchard Savanna of Beard (1953), occupies a rather restricted area in the Sierra, principally south and southwest of the Santa Marta massif and at elevations below 450 feet. The formation intergrades with both the Semi-Evergreen Seasonal Forest and the Deciduous Woodland where contact exists.



PLATE 12
Savanna on Volcán Santa Marta near Guasuntlan. May 1962, 200 feet.
Photograph by R. F. Andrie.

Ground cover within the savanna is of variable density and consists principally of grasses, sedges, and woody plants of which the most common are *Paspalum* spp., *Panicum* sp., *Dichromena ciliata*, *Rynchospora* spp., *Asclepias woodsoniana*, *Stemodia durantifolia*, and *Melanthera angustifolia*.

The formation is rather open. Common trees include *Curtella americana*, *Byrsonima crassifolia*, *Apeiba tibourbou*, *Quercus oleoides*, and *Spondias mombin* (Andrle, 1964). These attain maximum heights of 10 to 20 feet.

Epiphytes are uncommon. Although leaves of most trees are shed annually (usually at the end of the dry season, May, or after the passage of fire), the trees never remain leafless for any extended length of time.

The reasons for the existence of this formation are debatable as they are for most other tropical savannas. Budowski (1959) states that experimental evidence indicates that all savannas would revert eventually to forest if fire is precluded from the area and if a seed source is near. However, there is not universal agreement on this matter. Beard (1953) states that "savanna may be characterized as the vegetation of the highly mature soils of senile land formations . . . which are subject to unfavorable drainage conditions in the form of intermittent perched water tables, with alternating severe periods of water logging and dessication." Furthermore, he continues and states that although the savanna may be swept by regular fires and the vegetation be adapted as to be fire resistant, the vegetation is not dependent upon fire for its maintenance but is an edaphic climax.

The Beard hypothesis seems to be the more reasonable explanation for the existence of the savanna in the Sierra. First, the formation occurs in one of the most ancient geological areas in the range (the Santa Marta massif) and the grey to black clay soils probably indicate severe leaching has occurred (Friedlaender, 1923). Second, the land is of low relief and there are numerous outcroppings of bedrock, two factors that probably make drainage relatively inefficient. Third, the annual precipitation, as recorded at Guasuntlan, averages approximately 67 inches and there are at least five months of the year that receive less than four inches of rainfall (Andrle, 1964). Fourth, the area has very few human inhabitants (and probably has had very few in the past) and so man-caused fires are relatively uncommon.



PLATE 13

Deciduous Woodland on Volcán Santa Marta near Soteapan, June 1965,
11,700 feet.

NOTICES

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THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

Volume 14

Number 3

September, 1975

IN THIS ISSUE

- Courtship and mating behavior of the
Fiery Skipper, *Hylephila phylaeus* (Hesperiidae)
Irene Shapiro 125
- Variability of courtship of the Buckeye Butterfly,
Precis coenia (Nymphalidae)
James A. Scott 142
- Variation in *Colias alexandra christina* Edwards
(Pieridae) in Southwest Manitoba
John H. Masters 148
- The role of watercress, *Nasturtium officinale* as a
host of native and introduced pierid butterflies
in California
Arthur M. Shapiro 158
- An ecological study of the butterflies of
the Sierra de Tuxtla in Veracruz, Mexico
(continued)
Gary N. Ross 169

THE JOURNAL
OF RESEARCH
ON THE LEPIDOPTERA

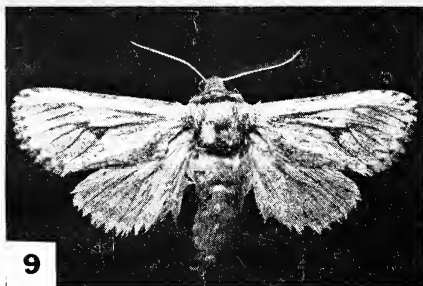
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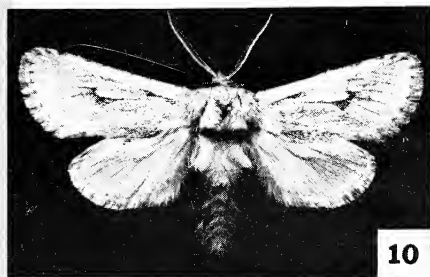
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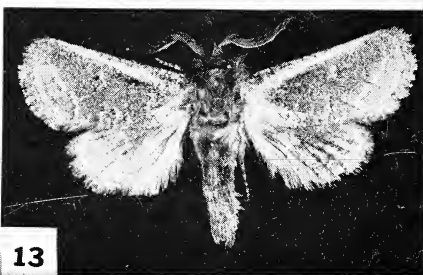
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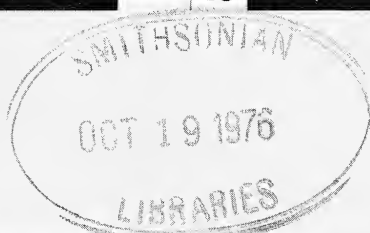
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12



13



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A REVISION OF
THE NORTH AMERICAN COMADIA

(COSSIDAE)

RICHARD M. BROWN

1055 Plaza Drive
Martinez, California 94553

THIS PAPER IS THE RESULT of my attempt to confirm and place in the genus a species that was described as *Comadia suaedivora* Brown and Allen (1973). During this work I discovered the lack of any recent literature and the existence of many specimens, mostly from California, that did not fit the previously described species.

The material used in this study was borrowed from the following institutions: California Academy of Sciences, San Francisco; Canadian National Collection, Ottawa, Ontario; Carnegie Museum, Pittsburgh, Pennsylvania; The American Museum of Natural History, New York; California Department of Agriculture, Sacramento; Los Angeles County Museum of Natural History, Los Angeles, California; University of California, Berkeley; United States National Museum, Washington, D.C.

Approximately 450 specimens were used in this study, including the Allotype of *Heterocoma albistriga* Barnes & McDunnough, the genitalia of the Holotype of *Comadia bertholdi bertholdi* (Grote), and a number of paratypes of various other species. Dr. Ronald W. Hodges kindly compared specimens to additional material in the U.S. National Museum.

COMADIA BARNES AND McDUNNOUGH

Bombyx Linnaeus, 1785, *Syst. Nat.*, 1:496.

Zeuzera Latreille, 1804, *Nouv. Dict. d'Hist. Nat.*, 24:186.

Hypopta Hübner, 1816, *Verz. beck. Schmett.*, pg. 195; Neumoegen & Dyar, 1893, *Journ. N. Y. Entomol. Soc.*, 1:32; *ibid*, 1894, *Journ. N. Y. Entomol. Soc.*, 2:164.

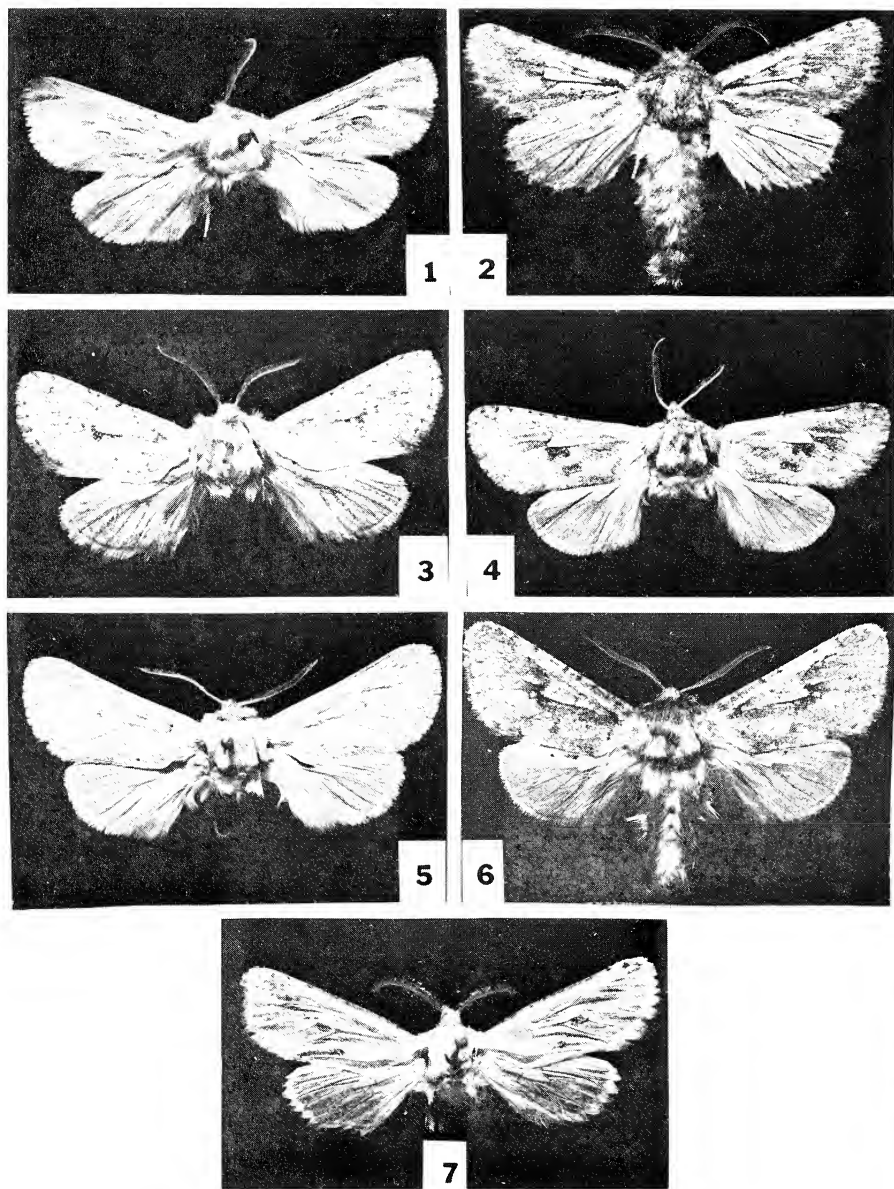


Fig. 1, *Comadia henrici*, Blyth, Riverside Co., California; Fig. 2, *Comadia suaedivora*, paratype, Tipton, Tulare Co., California; Fig. 3, *Comadia doli*, Soldier Meadows, Humboldt Co., Nevada; Fig. 4, *Comadia intrusa*, Santa Monica, Los Angeles Co., California; Fig. 5, *Comadia arenae*, Holotype, Wheeler Spring, Ventura Co., California; Fig. 6, *Comadia subterminata*, Tonto Creek Camp, Gila Co., Arizona; Fig. 7, *Comadia speratus*, Holotype, Madera, Madera Co., California.

Comadia Barnes & McDunnough, 1911, *Contrib. Natur. Hist. Lepid. of N. Amer.*, 1:26-29; Barnes & Benjamin, 1923, *Contrib. Natur. Hist. Lepid. of N. Amer.*, 5:88-96.

Heterocoma Barnes & McDunnough, new synonymy, 1918, *Contrib. Natur. Hist. Lepid. of N. Amer.*, 4(2):179; McDunnough, 1939, Check List of Lepid. of Canada and U. S. Amer., Part 2, *Microlepid.* pg. 62.

Head: proboscis absent; clypeus flat, level with or recessed below level of eyes. Male antennae bipectinate to end, pectinations arising from middle of segments on ventral half, each pectination with inner surface pubescent, terminating with one seta, a dorsal nob with one seta three fourths from base; female antennae serrate, shallowly bifid, each terminating with one or two setae. Thorax: epiphysis simple, less than tibial length; hind tibiae swollen; all spurs present. Wings (fig. 15): forewing Sc. free, R_1 from middle of discal cell, R_2 from top of areole, R_3 from end of areole, R_4 and R_5 stalked from R_3 , M_1 usually from top angle of discal cell, M_2 and M_3 from below center of discal cell, A_1 and A_2 free; hindwing Sc. free, R and M_1 usually from a point, but may be separated or stalked, Cu_1 from lower angle of discal cell, Cu_2 from bottom of discal cell, A_1 , A_2 , and A_3 free; cellula intrusa in both wings. Abdomen clothed with long hairs laterally lengthened. Male genitalia (fig. 17); harpé upturned, more or less squared posteriorly, inner surface slightly excavated; valvula with strong hooked process at base just below the costa; tegumen broad, hood shaped with 2 to 6 setae at anterior corners of base; uncus small, deflexed as a short, strong hook; gnathos spoon shaped with long diverging arms; aedeagus as simple sclerotic tube slightly deflexed from middle, without internal sculpturing. Female genitalia (fig. 16); ovipositor simple, long and tapering; posterior and anterior apophysis long, well developed; ovipositor lobe densely covered with setae, as is posterior edge of segment 8; ductus bursa and bursa membranous, without any chitinated structure.

KEY TO THE SPECIES OF *COMADIA*

(Based on male characters)

1. Both wings light buff or cream colored; without dark brown discocellular spots2.
- Both wings pale gray to dark gray or brown, with or without dark brown discocellular spots3.

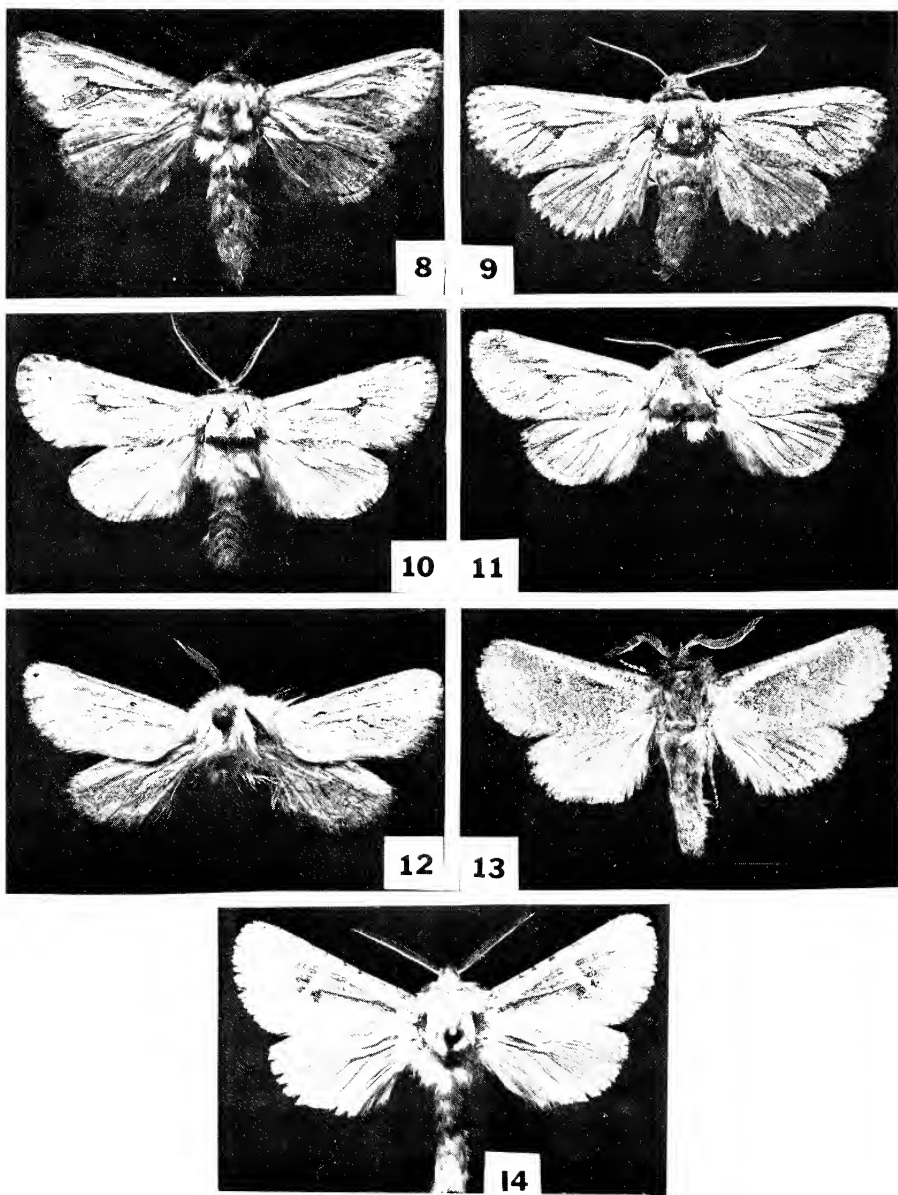


Fig. 8, *Comadia bertholdi indistincta*, Holotype, 8 mi. w. Fort Jones, Siskiyou Co., California; Fig. 9, *Comadia bertholdi polingi*, Kenworthy, Riverside Co., California; Fig. 10, *Comadia bertholdi polingi*, paratype, Bent, Otero Co., New Mexico; Fig. 11, *Comadia alleni*, Holotype, La Grange, Stanislaus Co., California; Fig. 12, *Comadia manfredi*, Oro Blanco Mts., Santa Cruz Co., Arizona; Fig. 13, *Comadia redtenbacheri*, Big Bend National Park, Brewster Co., Texas; Fig. 14, *Comadia albistriga*, Alamogordo, Otero Co., New Mexico.

2. Wings not more than 10 mm. long, cream colored, immaculate, epiphysis one half tibia length*manfredi*.
Wings at least 12 mm. long, light buff with white markings; epiphysis greater than one half tibia length*henrici*.
3. Upper forewing with at least some dark discocellular scaling present; wing not crossed by lines formed by bicolored scales4.
Upper forewing without discocellular scaling; wing crossed with numerous lines formed by an alignment of bicolored scales; epiphysis quite short*redtenbacheri*.
4. Discocellular spot divided by prominent whitish discal bar extending to Cu₂ in the tornal area; a white bar along cubital vein to discal bar; white subterminal line; epiphysis minute or missing*albistriga*.
Upper forewing not so divided by white bar; epiphysis well developed5.
5. Upper surface of wings dark gray to brown6.
Upper surface of wings silver gray to white8.
6. Upper forewing with subterminal line; discocellular spot covering entire end of discal cell (Utah, Colorado, Arizona, New Mexico)*subterminata*.
Upper forewing usually without postmedial line; discocellular spot reduced to lower angle of discal cell (California) 7.
7. Upper forewing heavily dusted with gray; subcosta very white, discal cell with some white (San Joaquin Valley)*suaedivora*.
Upper forewing lightly dusted with brown scaling; subcosta concolorous to wing, not white (coastal Southern California)*intrusa*.
8. Upper forewing pale tan or buff with scattered brown scales; veins lightly marked; discocellular spots relatively undefined; usually with some indications of subterminal lines*dolli*.
Upper forewing more gray or white; without general scattering of dark scales; discocellular spots well defined, but may be reduced in size9.
9. Upper forewing light gray; discocellular spot greatly reduced, restricted to lower distal corner of discal cell*arenae*.
Upper forewing light gray or white; discocellular spot prominent10.

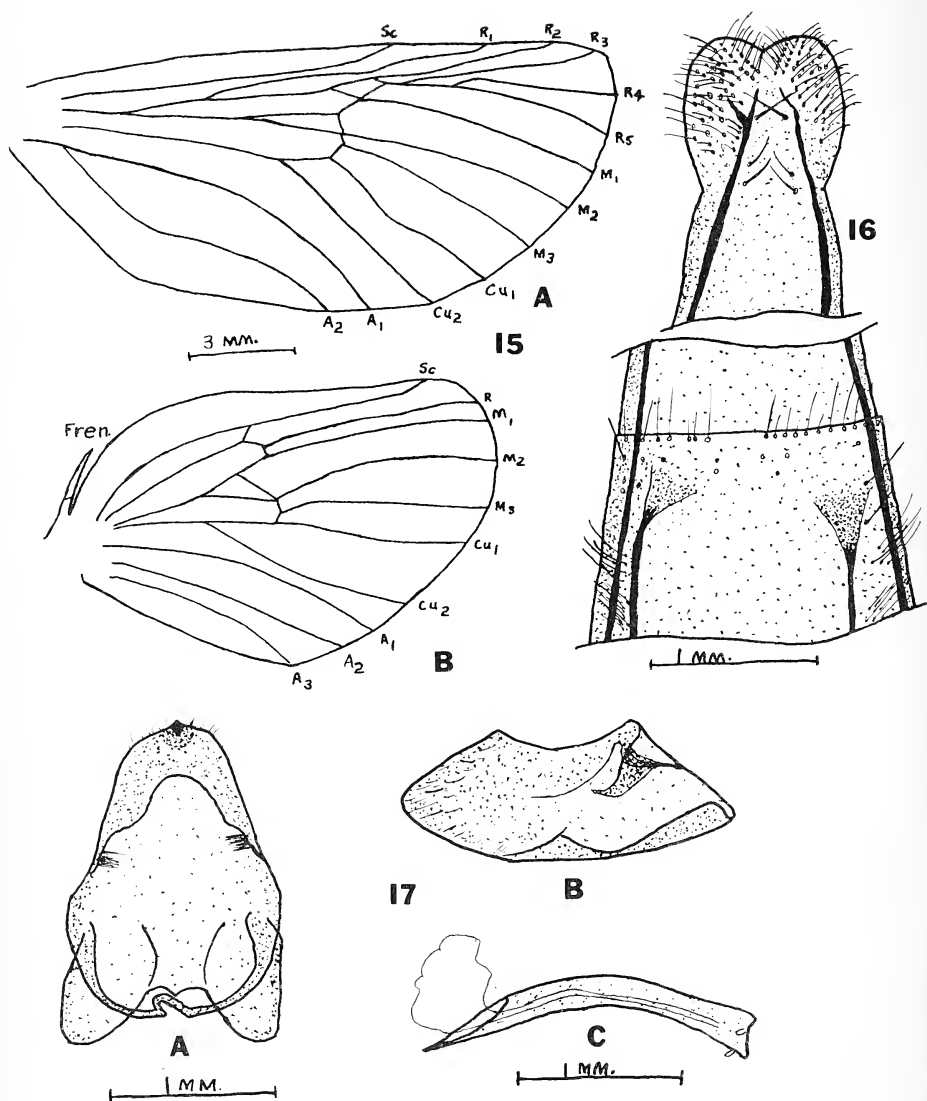


Fig. 15, Wing venation: A, right forewing, B, right hindwing; Fig. 16, Female genitalia; Fig. 17, Male genitalia: A, tegumen with gnathos and uncus, B, left harpé, C, aedeagus.
Distributional maps for *Comadia*.

10. Upper forewing white; veins unlined with dark brown11.
Upper forewing grayish; veins usually lined with dark brown, except for *bertholdi indistincta*12.
11. Discocellular spot dark, defined and contrasting with white wing; overlay of gray restricted to submarginal and apical region*speratus*.
Discocellular spot poorly defined; upper forewing with overlay of gray heavy except for submarginal and discal area, which is white*alleni*.
12. Discocellular spot restricted to lower angle of discal cell; veins lined dark to margin (Great Basin Region)13.
Discocellular much reduced; veins unlined (North and Coastal California)*bertholdi indistincta*.
13. Upper forewing light gray to cream with light suffusion of dark brown; subcosta and discal cell very white; median vein at base of discal cell dark brown; fringe well checkered at end of dark veins*bertholdi polingi*.
Upper forewing gray with heavy suffusion of dark brown; subcosta and discal cell with general wing suffusion; median vein at base of discal cell with dark brown greatly reduced or missing; fringe lightly checkered at end of dark veins*bertholdi bertholdi*.

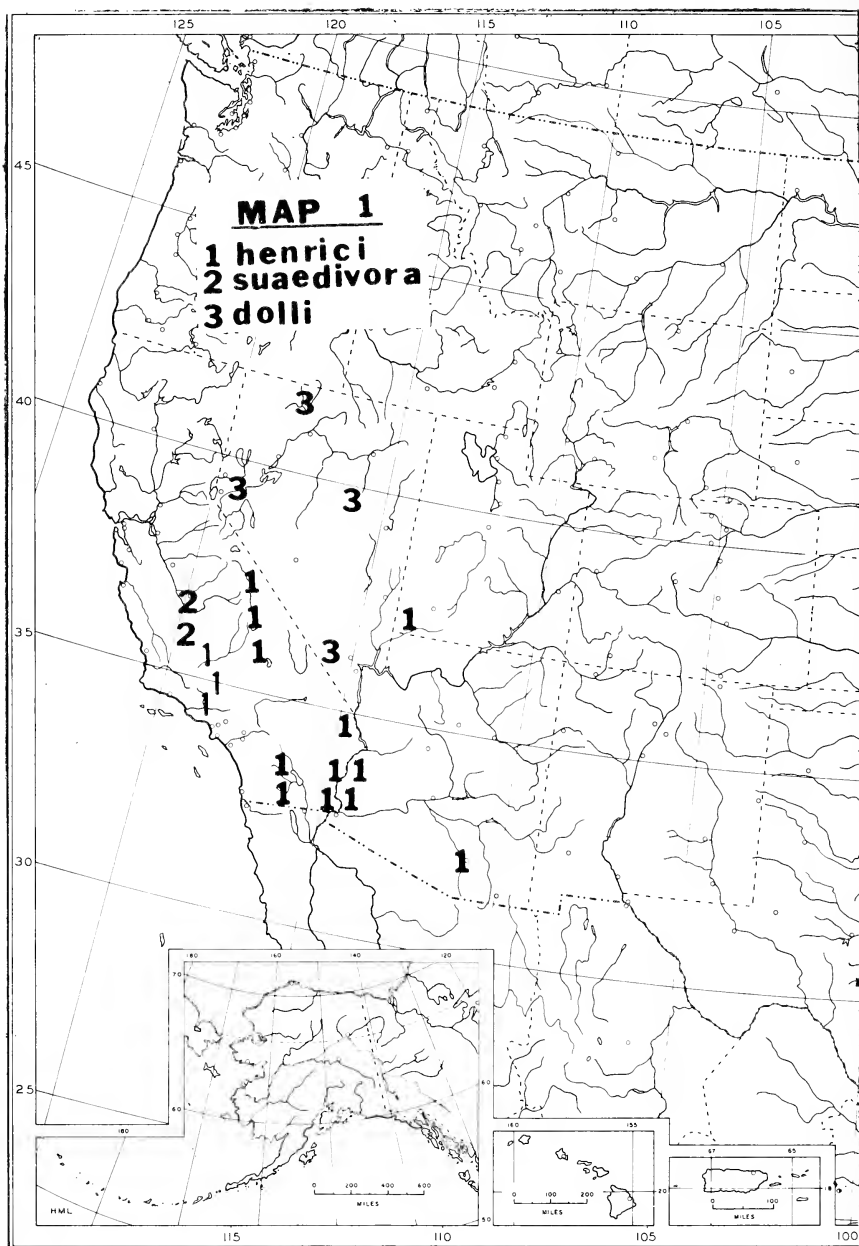
COMADIA HENRICI (Grote)

(fig. 1 ♂)

Hypopta henrici Grote, 1882, *Papilio*, 2:31; Dyar, 1902, *Bull. U.S.N.M.*, 52:363; Neumoegen & Dyar, 1893, *Journ. N. Y. Entomol. Soc.*, 1:33; *ibid.*, 1894, *Journ. N. Y. Entomol. Soc.*, 2:165; Holland, 1903, *Moth Book*:379, Pl. 12, Fig. 3; Dyar, 1937, in Seitz, *Macrolepidoptera*, 6:1275, Pl. 182.

Comadia henrici; Barnes & McDunnough, 1911, *Contrib. Natur. Hist. Lepid. N. Amer.*, 1:28, Pl. 5, fig. 5; *ibid.*, 1917, *Check List of the Lepid. of Boreal Amer.*: 195.

Male: Head, thorax and abdomen light cream colored; longest antennal pectination four times shaft width; antennal pectination/eye diameter ratio average is .42; epiphysis/tibia ratio average is .67. Upper surface of wings, costa with buff scales scattered or in spots to apex; subcosta white; area between radial and cubital veins to submarginal area buff; remainder with buff spots between veins; basal half of cell M_3 white, remainder buff; cell Cu_1 buff to fringe; basal two thirds of cell Cu_2 and anal cell



buff. All veins white; fringe white. Hindwings uniformly light cream, veins may be slightly darkened. Under surface of wings, with forewing costa somewhat darker than upper surface; dark scaling more diffuse, following general pattern of upper surface; hindwing concolorous to upper surface. Female; similar to male; abdomen longer, heavier. Wing size in male 12-15 mm; in female 16-20 mm.

Range.—California, Arizona, Utah, see map # 1. Flight period, March through May.

This species is recognized by its pale cream and buff color. The antennal pectination in the California specimens are slightly shorter than in those from Arizona and Utah. This species has the longest epiphysis in the genus. Of the 116 specimens examined, the majority are from Southern California.

COMADIA SUAEDIVORA Brown & Allen

(fig. 2 ♂)

Comadia suaedivora Brown and Allen, 1973, *Pan-Pacif. Entomol.*, 49:240.

Male: Head and thorax with mixture of white and brown scales; longest antennal pectination three times shaft width; antennal pectination/eye diameter ratio average is .42; epiphysis/tibia ratio average is .59. Upper forewing mostly fuscous; subcostal to subapex with discal cell invaded by white; discocellular spots reduced and restricted to lower angle of discal cell; usually a faint postmedial line present. Hindwing concolorous with abdomen. Under forewing costa with basal three-fifths dark brown, remainder white; dark subapical spot; postmedial line present; distally dark between veins. Hindwing creamy white with dark brown suffusion. Female: Similar to male, somewhat darker and larger. Wing size in male, 12-16mm; in female 12-17mm.

Early stages.—Brown and Allen (1973) reported that the larvae feed gregariously in the crown and roots of *Suaeda fruticosa* (L.) Forsk. The larva is rose-lavender colored with a heavily sclerotized horn on the dorsal surface of the anal flap. The pupa is dark brown and heavily spined. Pupation occurs in a subterranean chamber, but prior to emergence the pupa leaves the chamber and extends part way above the ground surface.

Range.—San Joaquin Valley in California, see map #1. Flight period, May and June.

Comadia suaedivora is nearly the darkest species in the genus, only *subterminata* is darker. However, *suaedivora* is differentiated by its white subcosta, contrastingly lighter hindwings and geographical distribution. Number of specimens examined, 99.

COMADIA DOLLI Barnes & Benjamin

(fig. 3 ♂)

Comadia dolli Barnes & Benjamin, 1923, *Contrib. Natur. Hist. Lepid. N. Amer.*, 5:90.

Hypopta dolli; Dyar, 1937, in Seitz, 6:1275.

Male: Head with cream and brown scales; antennae with cream colored scaling to end, longest antennal pectination is 2.5-3.0 times shaft width; antennal pectination/eye diameter ratio average is .36; epiphysis/tibia ratio average is .59. Thorax cream colored; collar blackish; partagia tipped in black. Abdomen lighter in color than thorax. Upper wings, ground color creamish-white; costa checkered, subcosta to subapical and upper part of discal cell white; rest of wing with scattered brown scales; discocellular spots reduced, with only the veins outlined darker, except for Cu_1 and Cu_2 which are whitish; end of veins brown; fringe checkered at end of veins. Hindwings concolorous or slightly darker, veins lined darker. Under wings cream to fuscous; fore and hindwings concolorous. Female: Wing length same as in the male, abdomen longer; upper surface forewing with discocellular cell wanting; wing scattered with brown scales, some forming short reticulations between veins. Hindwings as in male. Wing size 12-15mm.

Range.—California, Nevada, see map #1. Flight period, April through July.

This moth has the patches at the end of the discal cell reduced and restricted to the lower angle and cubital veins. *Comadia dolli* is very close to *bertholdi* in size and markings, but has longer antennal pectinations, longer epiphysis and a tendency to subterminal lines. Also, *dolli* tends to have a cream coloration similar to *henrici*, as opposed to the gray-white of *bertholdi*. Number of specimens examined, 16.

COMADIA INTRUSA Barnes & Benjamin

(fig. 4 ♂)

Hypopta bertholdi; Rivers, 1897, *Psyche*, 8(249):10; Dyar, 1897, *Psyche* 8(249):10; Holland, 1903, *Moth Book*:379, Pl. XII fig. 2.

Comadia intrusa Barnes and Benjamin, 1923, *Contrib. Natur. Hist. Lepid. N. Amer.*, 5:92.

Hypopta intrusa; Dyar, 1937, in Seitz, 6:1275.

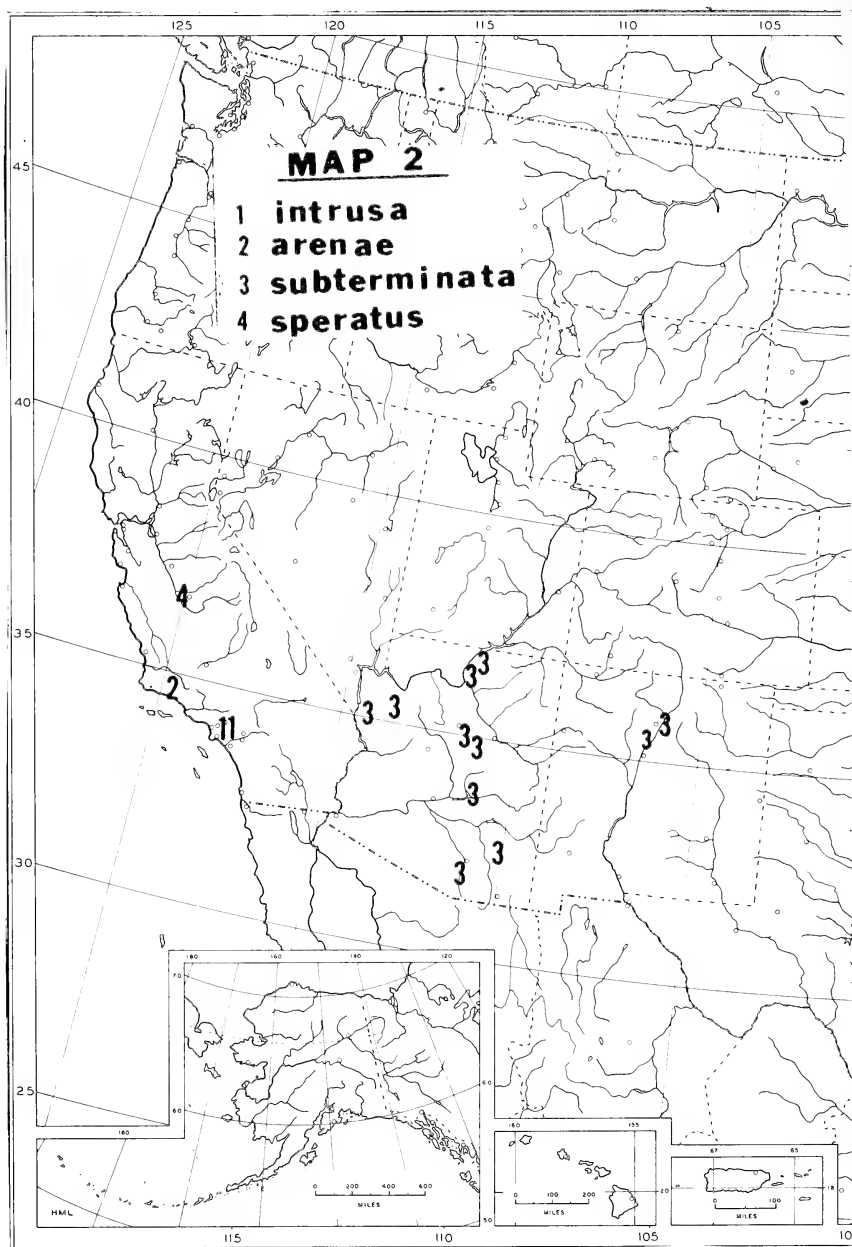
Male: Head and thoracic vestiture with white and dark-brown scales; longest antennal pectinations two times shaft width; antennal pectination/eye diameter ratio average is .29; epiphysis/tibia ratio average is .59; abdomen not darker than thorax. Upper forewing white with a light scattering of pale brown; discocellular spots pale and diffuse; veins outlined darker brown; reticulated submargin present. Hindwing light fuscus. Under forewing with costa checkered or solid brown on basal half, remainder white; remainder ventral surface fuscus. Under hindwing concolorous with forewing. Female: Larger, with markings less defined than in male. Wing size in male 13-17mm; female 20mm.

Early stages.—Rivers (1897) in his brief account of the larvae of "*Hypoptya bertholdi* Grote" reports that its food "consists of the fibre of the main stem and larger roots of the lilac flowered lupin," and that the presence of larvae of different ages in the same plant implies that larval growth extends beyond one year. The larvae wander some distance from the plant and pupate in a subterranean chamber more than one foot deep. Just prior to eclosion the pupa extends part way above the ground surface.

The color of the larva when about one half inch long is a yellow white, but when larger it becomes a bright carnelian red, heightened by an enameled surface (Rivers, 1897). Additional characterization of the larvae by Dyar (1897) tells of the body being ventrally flattened, with a large black recurved horn above on the anal flap. Thoracic legs are small and pointed; abdominal legs are very short with crotchets distinct and arranged in two long parallel transverse rows.

Range.—California, see map #2. Flight period, June through August.

Dyar (1897) followed Rivers (1897) in recognizing the southern California larvae as *Hypoptya bertholdi* Grote, not realizing an undescribed species was involved. Holland (1903) figured a female he called *H. bertholdi*. I have a female *intrusa* from the Holland collection labeled "Moth Book Plate XII, fig. 2," that matches the specimen in the plate. Some *intrusa* strongly resemble *subterminata*, but do not have dark suffusion or the prominent reticulations found in *subterminata*. The antennal pectination in this species is the shortest found in *Comadia*. Specimens examined, 11.



COMADIA ARENAE Brown, new species

(fig. 5 ♂)

Male: Head and thorax whitish-gray with a few brown scales; antennal shaft dorsally scaled, longest pectination twice the shaft width; antennal pectination/eye diameter ratio average is .29; epiphysis/tibia ratio average is .55. Abdomen concolorous with thorax. Upper forewing concolorous with body; discocellular spot represented by a few dark brown scales and ocher shading; base of cell Cu_1 ocher; middle of cell A_1 ocher; veins unmarked; fringe wide and white. Hindwings mouse-gray, veins lightly marked; fringe as on forewing. Under forewing costa with white and dark brown scales mixed to three-fifths from base, remainder white; remainder of wing light fuscous; fringe white. Hindwing lighter; fringe white. Wing length in Holotype 15mm; variation, 13-17mm.

Holotype male, California, Ventura County, Wheeler Springs, 29 July 1943, Don Meadows. Paratypes: 4 ♂, same locality and collector as holotype, 1 ♂, 21 July 1943, 1 ♂, 27 July 1943, 2 ♂, 29 July 1943. Type disposition: The Holotype and three paratypes are at the Los Angeles County Museum of Natural History, Los Angeles, California; one paratype at the California Academy of Sciences, San Francisco. See distribution map #2.

This species is somewhat variable, with the discocellular spot greatly reduced or absent. There is no dark scaling on the veins and no concentration of dark suffusion on the upper forewing; this gives a uniform, smooth appearance. Number of specimens examined, 5.

COMADIA SUBTERMINATA Barnes & Benjamin

(fig. 6 ♂)

Comadia subterminata Barnes and Benjamin, 1923, *Contrib. Natur. Hist. Lepid. N. Amer.*, 5:91.

Hypopta subterminata; Dyar, 1937, in Seitz, *Macrolepidoptera*, 6:1275.

Comadia bertholdi fusca Barnes and Benjamin, 1923, *Contrib. Natur. Hist. Lepid. N. Amer.*, 5:92.

Male: Head, palpi, front and vertex concolorous with or darker than thorax; thorax with mixture of black and white vestiture; longest antennal pectination 2.5-3.0 times shaft width; antennal pectination/eye diameter ratio average is .36; epiphy-

sis/tibia ratio average is .56. Upper forewing with ground color fuscus gray; costa with dark brown checks, in some specimens becoming a solid border; subcostal area and discal cell whiter; submarginal area with reticulations, usually consisting of one line that fades before reaching inner margin; discocellular spots quite heavy, extending cephalad to radials and caudad to vein A_2 ; veins lined with brown. Hindwings light fuscous with veins lined darker. Under forewing costa dark brown, broken by two or three white spots two thirds out from base; remainder of wing fuscus. Under hindwing same as upper surface. Female: Larger than male, markings similar to male, but less distinct. Wing length in male, 13-18mm; in female 19-21mm.

Range.—Utah, Colorado, Arizona and New Mexico, see map #2. Flight period, March through July.

This species is closely related to *bertholdi*, but is distinguished from *bertholdi* by its larger size (wing averages 2mm longer) and increased amount of dark scaling. Barnes and Benjamin (1923) described *fusca* as a subspecies of *bertholdi*. In a preliminary examination Rodald W. Hodges (in correspondence) suggested that *fusca* and *subterminata* were actually the same species; in my research I have been unable to find any reason to keep them separate species. Number of specimens examined, 24.

COMADIA SPERATUS Brown, new species
(fig. 7 ♂)

Male: Head, thorax white with pale fuscus shading about the collar; palpi quite black on the outer surface, white in inner surface; antennal shaft white scaled to tip; longest antennal pectination three times shaft width; antennal pectination/eye diameter ratio is .36; epiphysis/tibia ratio is .56. Abdomen white. Upper surface of wings with ground color very white; costa with dark brown scaling; discocellular spot at base of cells M_2 and Cu_1 ; a brown spot mid-cell A_1 ; heavy suffusion of dark brown between discal cell and apex; discal cell and subcosta with less dark scaling; fringe checkered. Hindwing mouse gray, veins darker. Under forewing costa black three fifths out from base, remainder white; remainder of wing fuscus except for discal cell. Hindwing costa white; remainder of wing concolorous to forewing. Female unknown. Wing length in holotype, 15mm.

Holotype male, California, Madera County, Madera, 14 May 1962, H. E. Gleason. Paratypes, 2 ♂, same data as Holotype. See distribution map #2.

Type disposition.—The Holotype is at the California Academy of Sciences, San Francisco. Two paratypes are at the California Department of Agriculture, Sacramento.

This is the whitest of all the *Comadia*. The black shading on the forewing when viewed together form a diagonal band across the wing. The white color of this moth readily distinguishes it from the other *Comadia*. Number of specimens examined, 4.

COMADIA BERTHOLDI (Grote)

Hypopta bertholdi Grote, 1880, *Bull. Brook. Entomol. Soc.* 3:45.

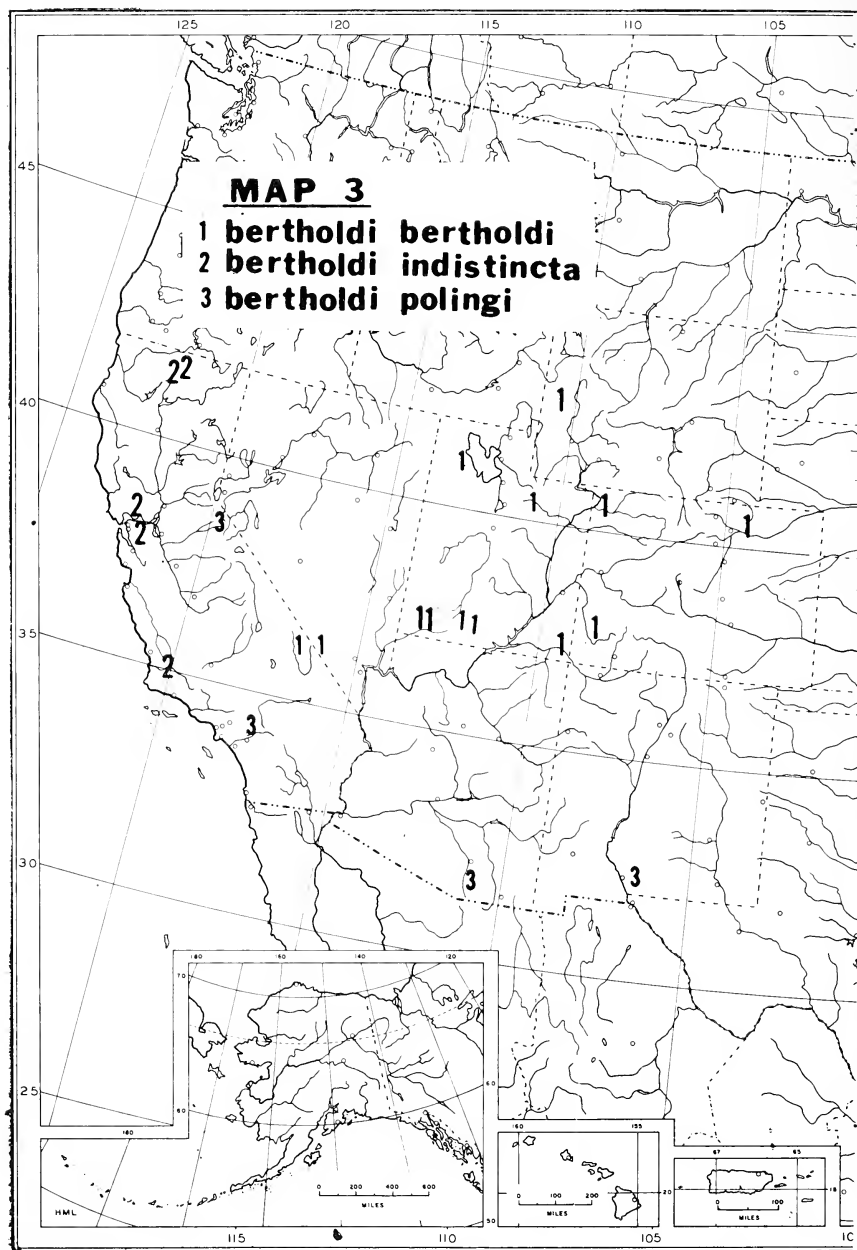
Male: Head and thorax with black and white mixed vestiture; abdominal color slightly lighter in color. Upper surface forewing from very light gray to a dark ash, with some black suffusion; heaviest suffusion obliquely from end of discal cell to apex; cubitus and end of discal cell caudad of M_2 dark brown; base cell Cu_1 and M_2 with scaling as on cubitus; base of cell M_3 usually without dark scaling; basal one third to one half of radius with dark scaling; remaining veins may or may not be lined in dark brown; fringe lightly checkered, beige to gray-brown. Under surface forewing costa dark brown or black; remainder of forewing and all of hindwing white to gray-brown. Female: Larger than male; ground color as in male; the dark color on the cubitus and at end of discal cell less distinct.

The slightly different maculation in each population of the variable species has caused the proliferation of names under the nominate subspecies. At present there are three subspecies; the nominate subspecies is from the Great Basin, *C. bertholdi polingi* is from the southwest and a new subspecies is from California.

COMADIA BERTHOLDI BERTHOLDI (Grote), new status (no figure)

Hypopta bertholdi Grote, 1880, *Bull. Brook. Entomol. Soc.*, 3:45; Neumoegen & Dyar, 1893, *Journ. N. Y. Entomol. Soc.*, 1:33; *ibid.*, 1894, *Journ. N. Y. Entomol. Soc.*, 2:165; Rivers & Dyar, 1897, *Psyche*, 8:10; Holland, 1903, *Moth Book*: 379, Pl. XII fig. 2; Dyar, 1937, in Seitz, *Macrolepidoptera*, 6:1275, Pl. 182; Dyar, 1902, *Bull. U. S. N. M.*, 52:363.

Comadia bertholdi; Barnes & McDunnough, 1911, *Contrib. Natur. Hist. Lepid. N. Amer.*, 1:27; *ibid.*, 1917, *Check List of the Lepid. of Boreal Amer.*: 195.



Hypopta edwardi Neumoegen & Dyar, 1893, *Journ. N. Y. Entomol. Soc.*, 1:32; Dyar, 1937 in Seitz, *Macrolepidoptera*, 6:1275; Dyar, 1902, *Bull. U. S. N. M.*, 52:363.

Comadia edwardi; Barnes & McDunnough, 1917, *Check List of the Lepid. of Boreal Amer.*: 195.

Comadia engelhardti Barnes & Benjamin, 1923, *Contrib. Natur. Hist. Lepid. N. Amer.*, 5:89.

Hypopta englehardti; Dyar, 1937, in Seitz, *Macrolepidoptera*, 6:1275, Pl. 182.

Comadia stabilis Barnes & Benjamin, 1923, *Contrib. Natur. Hist. Lepid. N. Amer.*, 5:90.

Hypopta stabilis; Dyar, 1937, in Seitz, *Macrolepidoptera*, 6:1275.

Male: Longest antennal pectination three times shaft width; antennal pectination/eye diameter ratio is .34; epiphysis/tibia ratio is .56. Upper surface of forewing with prominent dark suffusion; cubitus and end of discal cell caudad of M_2 with heavy dark brown scaling; remainder of wings as described in general characterization. Female as described. Length of forewing: male 13-16mm; in female 18-19mm.

Range.—California, Colorado, Wyoming, see map #3. Flight period, June through August.

This is the darkest of the three subspecies and the most variable. I have not seen *C. edwardi*, but have placed it as a synonym of *bertholdi bertholdi*. Barnes and Benjamin (1923) doubted the validity of *edwardi* as a species, believing it to be a color form or an aberrant individual. Neumoegen and Dyar (1893) in their original description state that the type is from Colorado, which lends support to this concept. Number of specimens examined, 45.

COMADIA BERTHOLDI INDISTINCTA Brown,
new subspecies
(fig. 8)

Male: Similar to *bertholdi bertholdi* except cubitus with dark markings reduced; markings at end of cell less distinct. Female: Larger than male; dark scaling so reduced that the wings are nearly immaculate. Wing length in Holotype, 16mm.; in Allotype, 18mm.

Early stages.—The Allotype and one female paratype are labeled "Lupinus", presumably the host of this species, as the

perennial lupine is the host for *C. intrusa* in Southern California.

Holotype male, California, Siskiyou County, 8 miles west of Fort Jones, 21 June 1971, F. D. Horn. Allotype, California, Contra Costa County, Orinda, 18 July 1949, E. G. Linsley. Paratypes: California, Contra Costa County: Orinda, 1 ♀, 18 July 1949, E. C. Clark; Kern County: Mt. Pinos, 1 ♂, 12 July 1953, Lloyd M. Martin; Napa County: Mt. Saint Helena, 2 ♂, 30 June 1956, W. R. Bauer and J. S. Buckett; Siskiyou County: Etna, 4 ♂, 16 July 1970; 3 miles east of Etna, 3 ♂, 11 July 1971, F. D. Horn. Holotype and allotype are deposited at the California Academy of Sciences, one paratype is in the collection of the Los Angeles County Museum of Natural History, one paratype is in the California Insect Survey, University of California, Berkeley, and the remainder are at the California Department of Agriculture, Sacramento. See distribution map #3.

This subspecies is distinguished from *b. bertholdi* by the reduced, indistinct brown discocellular spots. Antennal pectination/eye diameter ratio is .37; epiphysis/tibia ratio is .50. Number of specimens examined, 13.

COMADIA BERTHOLDI POLINGI Barnes & Benjamin,
new status

(figs. 9 ♂, 10 ♂)

Comadia polingi Barnes and Benjamin, 1927, *Pan-Pacif. Entomol.*, 4:67.

Male: Longest antennal pectination 2.5 to 3.0 times shaft width; antennal pectination/eye diameter ratio is .36; epiphysis/tibia ratio .48. Upper surface of forewing with reduced dark brown suffusion, white scaling prominent; subcosta to near apex without dark brown scales; costa dark brown, occasionally slightly checkered; dark brown of distal end of cell reduced; base of radial with dark brown streak about one fourth wing length. Hindwing slightly darker than forewing; veins lined dark. Under surface forewing with heavy brown suffusion except discal cell, which is paler. Under surface hindwing concolorous to upper surface. Female: Larger and with heavier brown suffusion than male. Wing length in male, 15-17mm; in female, 18-19mm.

Range.—Arizona, California, Nevada, New Mexico, see map #3. Flight period, May through August.

The white in *polingi* almost becomes a silver in some individuals. The brown scaling is always quite dark, but varies in amount present, thus, some specimens have the discocellular marking only on the veins. The over all darkness found in *bertholdi bertholdi* is not present. The range for *polingi* is around the southwestern edge of the Great Basin. Number of specimens examined, 40.

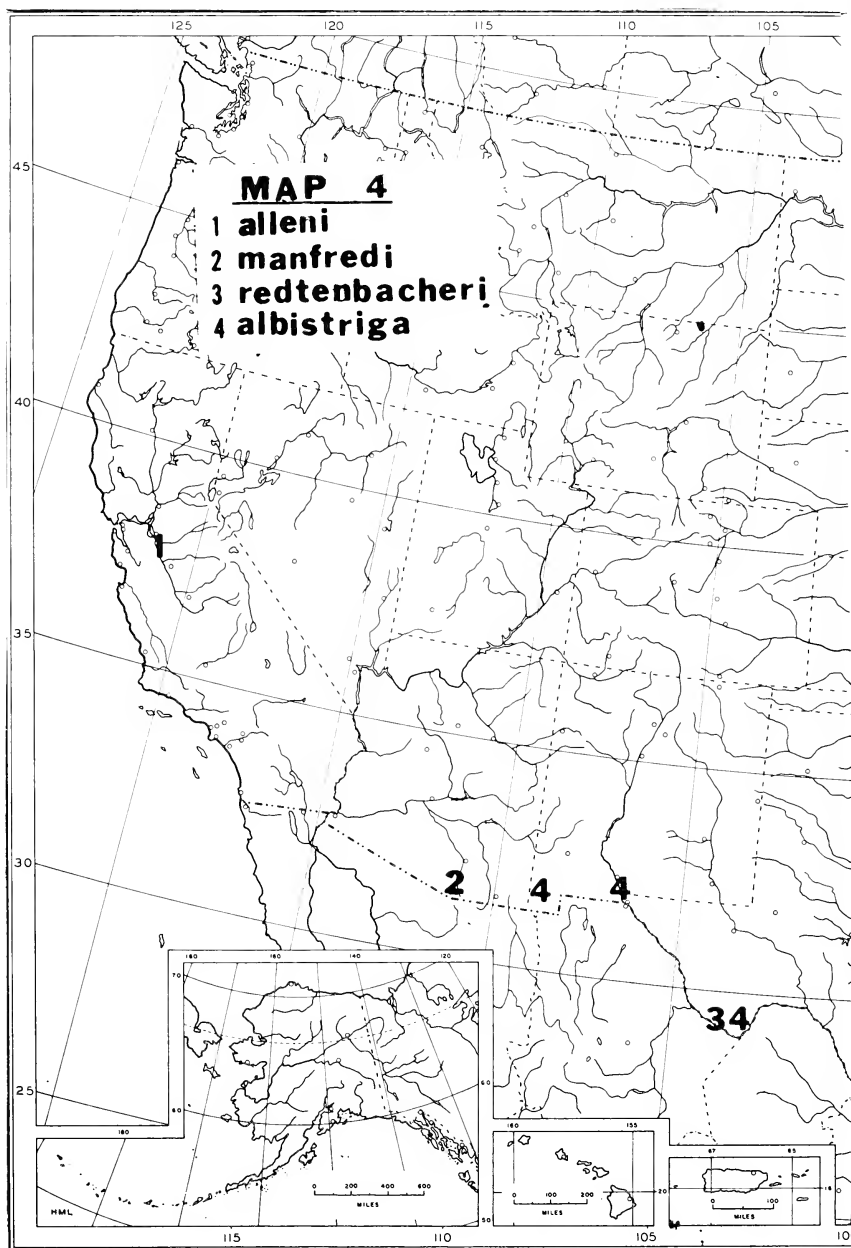
COMADIA ALLENI Brown, new species

(fig. 11 ♂)

Male: Head and thorax suffused with white and black scales; longest antennal pectination two times shaft width; antennal pectination two times shaft width; antennal pectination/eye diameter ratio is .43; epiphysis/tibia ratio is .5; antennal shaft white dorsally to apex. Forewing ground color white; oblique band of suffused fuscus from apex to end of discal cell; base of Radial vein with dark bar; Cubital vein and discocellular spot dark brown surrounded by ochre; middle of cell A_1 with spot of ochre and dark brown; veins outlined dark, checkered at end; fringe checkered. Hindwing fuscus, veins outlined dark; fringe white. Under side: forewing fuscus except for white over discal cell and subapically at costa. Hindwing lighter but fuscus at apex; veins dark. Female paler and slightly larger than male, almost immaculate. Wing length in Holotype 17mm; in allotype 18mm.

Holotype male, California, Stanislaus County, La Grange, 30 May 1960, R. P. Allen. Allotype, same locality and collector, 17 May 1968. Paratypes: same locality and collector as Holotype, 1 ♂, 11 May 1968; 1 ♀, 2 June 1960. Holotype and allotype are deposited in the California Academy of Sciences, San Francisco; paratypes are deposited in the California Department of Agriculture, Sacramento. See distribution map #4.

This species is nearly as white as *speratus* but *alleni* has heavier gray shading on the forewing in an area obliquely from the apex through the discocellular spot and out to the fringe. I am naming this species in honor of my good friend R. P. Allen. Number of specimens examined, 4.



COMADIA MANFREDI (Neumoegen)

(fig. 12 ♂)

Hypopta manfredi Neumoegen, 1884, *Papilio*, 3:139; Neumoegen and Dyar, 1893, *Journ. N. Y. Entomol. Soc.*, 1:33; *ibid.*, 1894, *Journ. N. Y. Entomol. Soc.* 2:164; Dyar, 1937, in Seitz, 6:1275; Dyar, 1902, *Bull. U. S. N. M.*, 52:363.

Comadia manfredi; Barnes and McDunnough, 1911, *Contrib. Natur. Hist. Lepid. N. Amer.*, 1:28; *ibid.*, 1917, *Check List of the Lepid. Boreal Amer.*, pg. 195.

Male: Head, thorax and abdomen covered with long cream colored hair; longest antennal pectination three times shaft width; antennal pectination/eye diameter ratio is .5; epiphysis/tibia ratio is .45. Upper fore and hindwings cream colored and devoid of all markings. Under forewing with a suffusion of dark along costa and subcosta; remainder of wing and hindwing concolorous with upper surface. Female unknown. Wing length in male, 11mm.

Range.—Arizona, see map #4. Flight period, May.

This species is the smallest and palest of all the *Comadia*, but has the longest antennal pectinations in the genus. From *henrici*, *manfredi* can be easily separated by its much smaller size, longer antennal pectination and shorter epiphysis. Specimens examined, 1.

COMADIA REDTENBACHERI (Hammerschmidt),

new combination

(fig. 13 ♂)

Zeuzera redtenbacheri K. E. Hammerschmidt, 1848, in *Naturwissenschaftliche Abhandlungen*, Gesammelt und Durch subscription von Wilhelm Haidinger, 2:151-152.

Bombyx agavis I. Blásquez, 1870, *La Naturaleza*, 1:285-288.

Hypopta agavis; L. Ancona, 1930, *Anales Del Instituto De Biología de la Universidad Nacional Autonoma de Mexico*, 1:265-277.

Hypopta chilodora H. Dyar, 1910, *Proceed. Natur. Mus.*, 38:270.

Hypopta redtenbacheri; Dyar, 1937, in Seitz, *Macrolepidoptera*, 6:1275, Pl. 181.

Male: Head, dorsal thorax, dorsal abdomen with tan and dark brown scaling; ventrally less dark; longest antennal pectinations 2.5-3.0 times shaft width; antennal pectination/eye diameter ratio is .42; epiphysis/tibia ratio is .26. Upper forewing, subcosta with narrow, very white strip from wing base to just short of apex; general color brown; wing scales tan at

base, dark brown at tip; two lines of raised scales cross wing; lines whitish on inner edge, dark brown on outer edge, lines formed by an alignment of these bicolored scales; inner line bent inward below discal cell; outer line out curved, parallel to fringe; terminal with a few scattered white scales; fringe scales very long, longest white and spatulate at end; shorter scales concolorous to wing, less spatulate. Hindwing uniform gray-brown; fringe as in forewing. Under forewing costa dark brown near base, mixed with white near apex; discal cell with some long hair-like white scales; remainder of wing uniform gray-brown. Hindwing as upper surface. Female: Generally larger and marked similar to male; lines of raised scales less contrasting and more numerous as short dashes; general ground color paler than male, due to the lack of dark tipped scales. Wing length in male, 12-14mm; in female 13-16mm.

Early stages.—The life history has been studied by Hammer-schmidt (1848), Blásques (1870), and Ancona (1930). The host is *Agavis salmiana* Otto, (*Ameryllidaceae*) (Ancona 1930). The eggs are laid near the base of the leaves of the host and are coffee colored at the time of emergence. Larvae are pale reddish in the first instar, becoming carmine in the later instars. The last tergite has a group of five spines forming a horn. The pupa has an array of spines that aid in digging to the ground surface prior to eclosion. In the regions of Mexico where *Agavis salmiana* is of economic importance, a 15% infestation of the host has been found (Ancona, 1930).

Range.—In the Big Bend area of Texas and wide spread within the boundaries of its host in Mexico. See map #4. Flight period, April and May.

I have placed this moth in this genus on the grounds the genitalia and wing venation are well within the generic limits. Ancona (1930), in his treatise of the larvae, placed this species in *Hypopta* and made Dyar's (1910) *chilodora* a synonym of *agavis*. Dyar (1937) placed both *chilodora* and *agavis* as synonyms of *redtenbacheri*.

Comadia redtenbacheri is distinguished by the color, and the lines of bicolored raised scales crossing the wings. *Comadia henrici* and *albistriga* tend to have some of the dark scales at the end of the discal cell bicolored, but since *redtenbacheri* does not have this discocellular spot there should be no confusion between species. Number of specimens examined, 16.

COMADIA ALBISTRIGA (Barnes & McDunnough),
new combination
(fig. 14 ♂)

Heterocoma albistriga Barnes and McDunnough, 1918, *Contrib. Natur. Hist. Lepid. N. Amer.*, 4(2):179; McDunnough, 1939, Check List of Lepid. of Canada and U. S. Amer. Part 2, *Microlepidoptera*, pg. 62.

Male: Head and dorsal thorax creamy white, mixed with black and brown scales; collar lightly marked with dark border; ventral thorax without dark scales; antennal shaft dorsally scaled, concolorous to thorax; longest antennal pectination three times shaft width; antennal pectination/eye diameter ratio average .48; epiphysis/tibia ratio average .21. Abdomen with dorsal anterior two thirds to three fourths mouse gray, remainder paler; ventral abdomen concolorous to ventral thorax. Upper surface of wings with forewing costa with brown checks; subcosta creamy-white without checks; discal area mouse brown; white postmedial line formed by staggered bars between veins; distal postmedial line paler; vein A_1 broadly creamy-white to fringe; discal spot large, creamy-white, extending to tornus; caudad A_1 concolorous to submarginal area; fringe pale checked at vein end; discocellular scaling dark brown. Hindwings uniformly mouse brown; fringe creamy-white without checks. Under surface of wings with forewing costa and fringe as above; remainder of wing mouse brown. Under hindwing marked as above. Female: Nearly immaculate, brown shading found in male only faintly visible. Wing length in male 11-14mm; in female 13mm.

Range.—Arizona, New Mexico, Texas, see map #4. Flight period, April and May.

Barnes and McDunnough (1918) were in error when they established the genus *Heterocoma* for *albistriga*, based mainly on the lack of a cellula intrusa and the presence of strongly stalked veins R and M_1 . There is variation among the individuals examined and *albistriga* is within the range of variation of *Comadia*.

Comadia albistriga can easily be recognized by the white bar crossing the wing from just below the costa through the brown discocellular spot to the tornal area. This line, when connected to the other three white lines, will form two triangles. Additionally, the upper forewing has variable reticulations formed by an alignment of dark brown tipped scales. These reticulations can be found any place on the wing except for the pale subterminal area.

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A NOTE ON *OENEIS MELISSA* (FABRICIUS)

IN THE WESTERN UNITED STATES (SATYRIDAE)¹

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OENEIS MELISSA (FABRICIUS) in the western United States has generally been referred to the subspecies *lucilla* Barnes and McDunnough in recent publications (Callaghan and Tidwell, 1971; Ferris 1971 a, b). The population in the Canadian Rocky Mountains was named *beani* by Elwes in his 1893 revision with Edwards of the worldwide *Oeneis*. The type locality is Laggan (Lake Louise) in Banff National Park, Alberta. The type locality for *lucilla* is Hall Valley, Park Co., Colorado.

Barnes and McDunnough, 1918, separated *lucilla* from the other subspecies of *melissa* on the basis of the following key characters: black palpi fringed with white dorsally, virtually no median (mesial) band on the ventral surface of the hind wings, and the "yellow" aspect of many specimens, especially in the females. Elwes in describing *beani* noted the blackish-brown aspect of the insect and its entirely black palpi.

Recent examination of specimens from the Rocky Mountains in the United States has demonstrated that both subspecies occur in this region. Material taken in Colorado, New Mexico and Utah (Leidy Peak, Uintah Co.) is *lucilla*. In Wyoming, *melissa* is found in the Wind River Range, Sublette Co. and on the Beartooth Plateau in Park Co. Specimens from these localities are the typical black-palpi *beani* found in Alberta. This subspecies has been recorded from Carbon Co. (Beartooth Plateau region), Glacier National Park, Montana and from Okanogan Co., Washington. To date, I have been unable to find any Idaho records.

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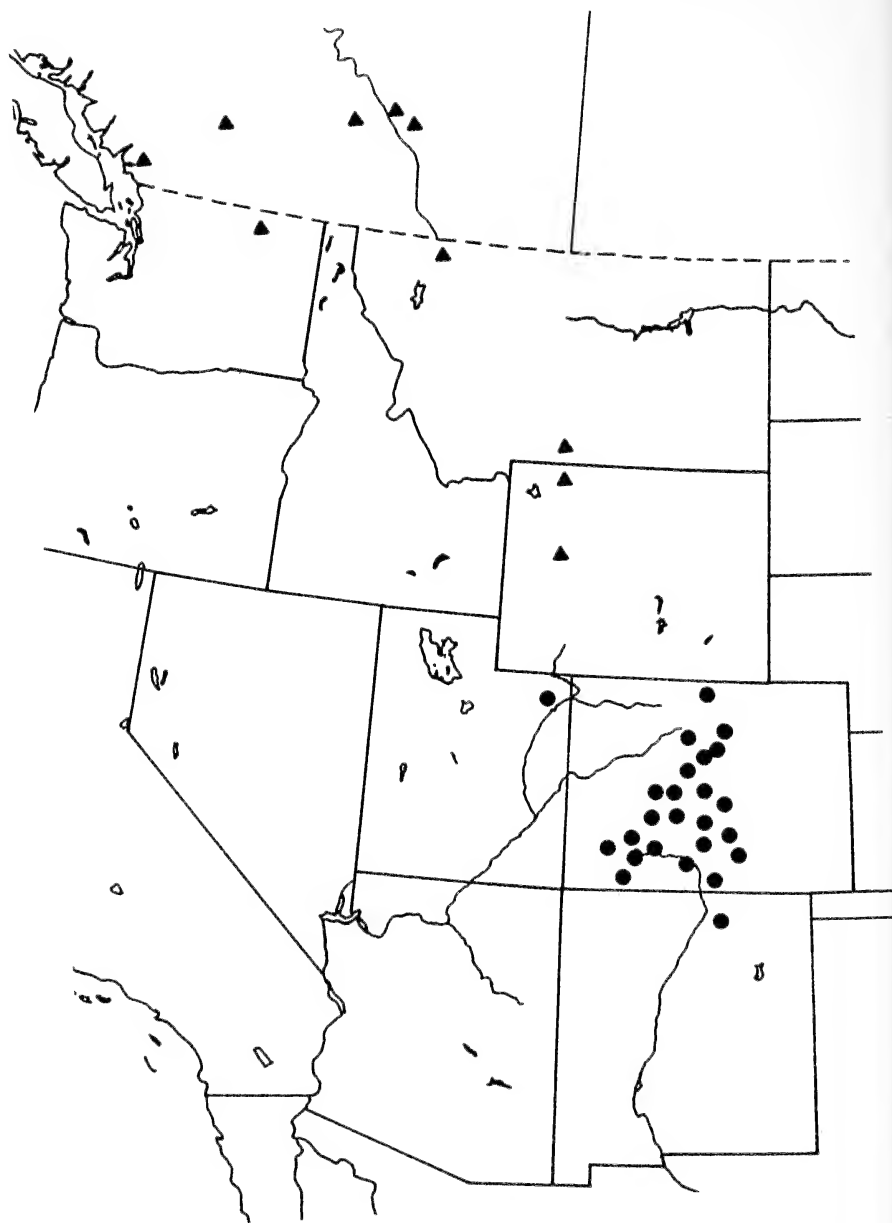


Fig. 1.—Distribution of *Oeneis melissa* in the western United States with partial records for southwestern Canada. Black dots = *lucilla*; black triangles = *beani*.

O. melissa beani frequents wind swept outcroppings of black or black-lichen-covered rocks above treeline. They are swift fliers and very wary. In the Beartooth Range, they occur at 11,000' and some 3000' lower on Plateau Mountain in southern Alberta.

Figure 1 illustrates the distribution of *melissa* in the United States. The Colorado county records include: Boulder, Chaffee, Clear Creek, Costilla, Custer, Fremont, Gilpin, Grand, Gunnison, Hinsdale, Huerfano, Lake, La Plata, Larimer, Ouray, Park, Pitkin, Rio Grande, Saguache, San Juan, San Miguel, Teller. In New Mexico, it is found in Taos Co.

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POST-PLEISTOCENE ENVIRONMENTS AND MONTANE BUTTERFLY RELICTS

ON THE WESTERN GREAT PLAINS

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FOR SEVERAL REASONS, a knowledge of the paleobotany of the western Great Plains has become increasingly important in understanding its butterfly fauna. Recent studies of many of its regional faunas (Brown *et al.*, 1957; Conway, 1966; Defoliart, 1956; Ferris, 1970a, 1970b, 1971; Johnson and Nixon, 1967; Johnson, 1972 (1973), 1975a; Nordin, 1967, 1968; Puckering and Post, 1960; and Scott, Ellis, and Eff, 1968) have placed a proper emphasis on the montane character of butterflies populating its non-riparian scarp woodlands and remaining climax coniferous forests. A rationale is needed to characterize these faunas in relation to their own elements as well as other faunas in the Nearctic (A. B. Klots and F. M. Brown, pers. com.). It is important to know whether they represent dispersal eastward from the Rocky Mountains, or if they are relicts of a former, more extensive, montane association in which unique allopatric populations of some montane Nearctic butterfly species occur, representing extreme divergence as peripheral populations. Similarly, understanding current ecological changes effecting their decline requires a knowledge of their probable origins (Johnson, 1976a).

Expanding distributional knowledge of taxa described from these areas, research presented in taxonomic studies (Ferris, 1973; Johnson 1976b, 1976c; Johnson and Balogh, 1976; Perkins and Perkins, 1967), and the recognition of important biological

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distinctions in some populations (Klots, 1975; and pers. com.) has indicated that many, if not most, of these scattered montane faunas are more related to each other than to faunas in the mountain ranges to their west. Thus, it is important to present paleobotanical evidence establishing this former montane association and to comment on its significance.

DISCUSSION

The major remaining conifer forest and montane areas of the Great Plains occur from western Nebraska northward. They include the Black Hills of South Dakota, the Pine Ridge of Nebraska, the Cheyenne Ridge of Nebraska and Wyoming (called the "three great pine relicts" by Clements, 1945) and the more limited scarps along the Niobrara River in Nebraska and the Little Missouri River in Montana and North Dakota. Of these, only the Black Hills remains in a climax condition.

The history of these areas, and thus a major part of the history of the Great Plains, is best understood by presenting a vegetative chronology since the Wisconsin glaciation. This evidence can then be used to explain the occurrence of the montane elements in its butterfly fauna:

The late Miocene, Pliocene, and early Pleistocene glaciations:

In the late Miocene and Pliocene the entire area was open woodland (savannah), with *Cedrella* (Meliaceae), and early *Celtis*, *Quercus*, *Mahonia*, *Pinus*, *Artemisia*, *Ambrosia*, and many *Asteraceae*. Montane areas, like the uplifted Black Hills, were coniferous forest and remained so throughout the four glaciations of the Pleistocene. The ice advances and interglacial episodes caused floral fluctuations probably not unlike those of the Wisconsin glaciation described below, which are most important in understanding present faunas.

Source: Wells, 1970.

The developing Wisconsin (before 20,000 years ago):

Boreal forests proceeded in bands before the glaciers. Periglacial winds formed a sand dune desert in central Nebraska from sand blown in from the Ogallala formation of the northern Great Plains. The Pine Ridge, Cheyenne Ridge, and other present-day uplands were not exposed at this time, but were in fact buried.

Sources: Schuchert, 1955; Smith, 1965; Wright, 1970.

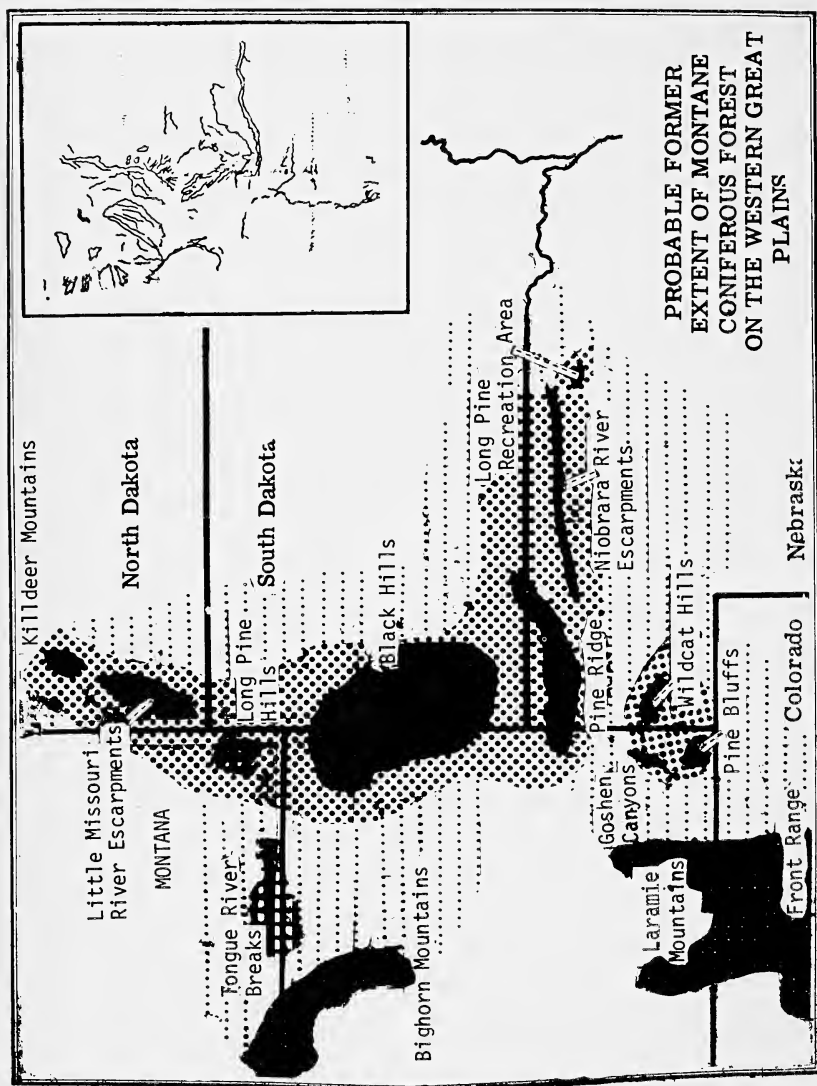


Fig. 1.—Map of western Great Plains area showing probable former extent of coniferous forest following the retreat of the Wisconsin glacier (dark stiples) and probable areas of pine-juniper open woodland during the same period (light stippled lines). Blackened areas represent present areas affording montane environments. Black areas with white cross-hatching represent areas of the Rocky Mountains. Areas of black cross-hatching show coniferous areas whose butterfly faunas are unknown. To the right above the title; the same region with lines representing present occurrence of scarp woodlands supporting pine (*Pinus ponderosa* Laws.) subclimax. The latter is the base map for noting butterfly distributions.

The full-glacial Wisconsin (14-20,000 years ago)

Boreal forest extended west to northeastern Kansas and northward across central Nebraska, but was prevented from reaching the Black Hills by the sand dunes. Instead, it continued westward across northwest South Dakota and north-central Wyoming. Montane *Pinus* climax forest covered the uplands westward. The present-day Pine Ridge, Cheyenne Ridge, and western North Dakota areas had now been exposed as uplands by the continual movement of loess eastward. Lowland pine-juniper open woodland occurred concentrically around the upland forests.

Sources: Wright, 1970; Wright and Ruhe, 1965.

The early glacial retreat (11-12,600 years ago):

Glacial retreat ended the periglacial winds. The sand dunes gave way to boreal forest which proceeded west to the present Black Hills. There, and in the Pine Ridge, Cheyenne Ridge, western North Dakota association, Niobrara River area, and associated lowland savannahs, it intermixed with montane coniferous forests. Contributed were still-surviving *Betula lenta* L., *B. papyrifera* Marsh., *Populus tremuloides* Michx., *Quercus macrocarpa* Michx., *Ostrya virginiana* Willd., *Ulmus americana* L. (pl. Clayt.), Willd., and *Corylus americana* Walt. The Big-horn Mountains were connected to the Black Hills by a moist (compared to today) *Pinus-Juniperus* savannah.

Sources: Morgan, 1963; Nixon 1967; Wells, 1970; Wright, 1970; Wright and Ruhe, 1965.

Mid-glacial retreat (10,000 years ago):

Further glacial retreat caused destruction of the boreal forest. Relicts survived in the Black Hills, Pine Ridge, and Niobrara escarpments. The extensive interplay of coniferous forest, open woodland, and prairie began. Montane coniferous areas were now nearly as shown in Figure 1.

Sources: McIntosh, 1961; Morgan, 1963; Nixon, 1967; Wells, 1970.

Post Wisconsin—the warm postglacial interval (9,500 to 1700 years ago):

Vast *Pinus* climax forests were evident as indicated in Figure 1.

Pinus dominated pine-juniper open woodland covered the present Sandhills of Nebraska and perhaps west-central North and South Dakota. Moist open woodland, predominantly *Juni-*

perus with some *Pinus*, connected the Laramie Mountains and Cheyenne Ridge, and the Bighorn Mountains and the Black Hills. A trend toward aridity began at the end of this period.

Sources: Deevy and Flint, 1957; Wells, 1970.

The woodland to semi-desert transition (1700-200 years ago):

Continuous coniferous forest began to recede. Pine climax retreated upland leaving subclimax relicts throughout various escarpments, but a climax forest in the Black Hills. In the face of increased aridity and prairie fires, open woodland began to give way to prairie.

Source: Wells, 1970.

Demise of the conifers (200 years ago to the present):

Continuous juniper and pine-dominated open woodlands came to an end. Conifers became nearly extinct in most areas, except remaining montane uplands. Mixed prairie and short-grass prairie disclimax prevailed over most areas; pine relicts remained limited to scarp woodland or the Black Hills.

Sources: Clements, 1945; Weaver and Albertson, 1956; Wells, 1965, 1970.

Figure 1 illustrates the probable maximum extent of former coniferous forest and pine-juniper open woodland on the western Great Plains in relation to existing nonriparian scarp woodlands. Distributions of species and subspecies endemic to these coniferous forests biomes are shown in figures 2 and 3. Figures 4 through 6 illustrate ranges of other montane entities still inhabiting the region, and probable relicts of two earlier fauna-influencing periods.

Examination of these data in relation to the chronology of paleobotanical events indicates evidence of five major elements influencing the existing butterfly fauna and its affinities:

1. Relicts of the boreal invasion and its associated deciduous flora (*L. eurydice* ssp., *P. batesii*, *N. vau-album j-album*).
2. Relicts of the extensive montane coniferous climax after the recession of the glaciers (*C. siva*, *C. meadii*, *C. alexandra krauthii*, *E. lucilius afranius*, *E. persius fredericki*, *E. ausonides palaeoreios*, *E. a. bernadetta*, *E. amyntula valeriae*, *G. piasus*, *H. pahaska pahaska*, *L. weidemeyerii oberfoelli*, *L. rubidus longi*, *N. ridingsii*, *N. menapia*, *P. phoebus dakotaensis*, *P. indra*, *P. muticaudatus*, *P. sisymbrii nordini*, *P. icarioides lycea*, *P. shasta minnehaha*, *P. satyrus*, *S. callippe*, *S. edwardsii*, *S. zerene*).

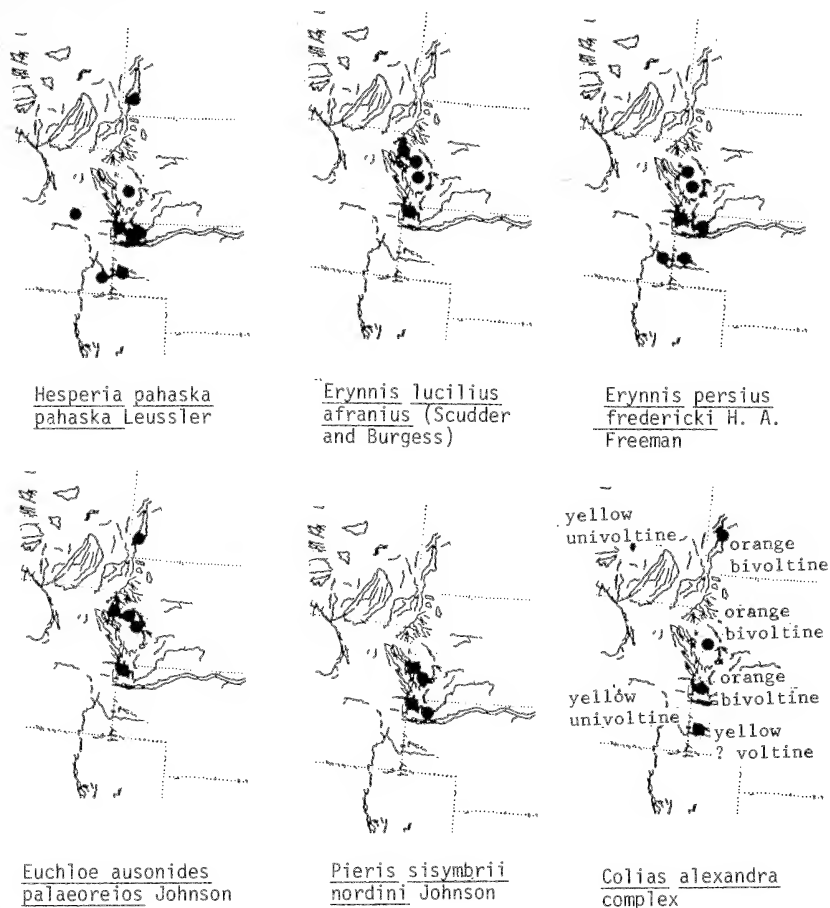


Fig. 2.—Distributions of species (includes only *Hesperia pahaska*) and sub-species (others) whose type localities are in one of the disjunct relict woodlands. Those clearly endemic are shown as such and usually represent montane coniferous forest entities. Others with more expansive distributions are usually montane grassland entities. Black lines on map indicate location of existing scarp woodlands in the region.



Limenitis weidemeyerii
oberfoelli Brown



Lycaena rubidus
longi Johnson and
Balogh



Plebejus shasta
minnehaha (Scudder)



Euphydryas anicia
bernadetta Leussler



Parnassius phoebus
dakotaensis Eisner

Fig. 3.—Same as Fig. 2.



Speyeria zerene
(Boisduval)



Polygonia satyrus
(Edwards)



Speyeria edwardsii
(Reakirt)



Speyeria callippe
meadii (Edwards)



Speyeria atlantis
(Edwards)



Speyeria coronis
(Behr)

Fig. 4.—Distributions of other montane butterflies on the western Great Plains in relation to existing scarp woodlands.



Papilio multicaudatus
Kirby



Papilio zelicaon
Lucas



Papilio rutulus
Boisduval



Papilio indra
Reakirt



Papilio bairdii
brucei Edwards



Neophasia menapia
(Felder and Felder)

Fig. 5.—Distributions of other montane butterflies on the western Great Plains in relation to existing scarp woodlands.



Calliophrys (Incisalia)
eryphon (Boisduval)



Callophrys (Mitoura)
siva (Edwards)



Plebejus icarioides
lycea (Edwards)



Glaucopsyche piasus
(Boisduval)



Oeneis uhleri
(Reakirt)



Cercyonis oetus
oetus (Boisduval)



Neominois ridingsii
(Edwards)



Cercyonis meadii
(Edwards)

RELICTS OF FORMER EASTERN
DECIDUOUS FOREST and NORTH-
WARD MONTANE INVASIONS



Phyciodes batesii (Reakirt)
Nymphalis vai-album j-album
(Boisduval & LeConte)
Lethe eurydice (Johannsen)

.....

Asterocampa celtis antonia
(Edwards)

Fig. 6.—Distributions of other montane butterflies on the western Great Plains in relation to existing scarp woodlands. Bottom right: listing of relict deciduous forest entities found in the Pine Ridge and representing extreme allopatry from their normal range.

3. Relicts of the northward dispersal of western montane entities (those above [2] but obviously *A. c. antonia*).
4. Relicts of montane entities once dispersed throughout the vast open woodlands (*C. siva*, *C. alexandra* ssp., *L. eurydice* ssp., *L. rudibus longi*, *P. multicaudatus*, *P. shasta minnehaha*, *S. edwardsii*).
5. The pattern of retreat of the coniferous forest at the beginning of the current aridity and fire-influenced period (all of the above, determining existing ranges).

These relationships show patterns important in interpreting the origin and faunal character of the insects of the region. All entities with habitats characteristic of montane coniferous forest, and with type localities within one of the now disjunct pine relicts, show a north-south distributional relationship within the former coniferous forest belt. Some are still found eastward along the Niobrara River where some limited scarp woodlands still support montane butterflies. Almost conversely, such entities, whose present distributions span the east-west arid basins, are grassland-related species, probably indicating the role of the open woodland in maintaining their ranges during the demise of the conifers, when montane forest entities retreated upland. Vast open woodland formerly in the Nebraska Sandhills, south of coniferous forest now isolated along the Niobrara River, figures as the origin of montane-related species which still occur there, in isolated and often unique environs like the post-climax prairie (Pool, 1914; Tolstead, 1941). In no case does a taxonomically distinct entity described from a montane conifer niche in the region show its primary relationship westward to the Rocky Mountains.

The most limited relict, small scarps which remain of the Cheyenne Ridge, contains montane representatives mostly with a northward relationship. However, some of its plains-adapted montane species evidence distinct interaction with populations clearly dispersed eastward from the Rocky Mountains. In strongly polymorphic *Colias alexandra* Edwards, evidence from Ferris (1973) and A. B. Klots (pers. com.) indicates the unique bivoltine and "orange" population called *C. a. krauthii* in the Black Hills does not extend southward and include the Cheyenne Ridge. Instead, a "yellow" population (of unclear voltinism) occurs here which seems more related to the "yellow" univoltine populations (called *C. a. alexandra*) on the plains sur-

rounding the Front Range in Colorado. Similarly, *Lycaena rubidus* Behr occurring on the plains south of the Pine Ridge shows purely northward related populations (*L. r. longi*) only in the pine-forested canyons of the region. Remaining populations on the plains, or in the limited remnants of the Cheyenne Ridge in Wyoming, show evidence of secondary intergradation with *L. r. rubidus* of the Rocky Mountains which has established many plains populations in eastern Colorado and Wyoming. The evidence of secondary intergradation in plains populations south of the Pine Ridge is shown in the geographic affinities of genitalic and wing pattern traits illustrated in Figure 7.

The great influence of the former extent of coniferous forest in the region can also be illustrated by the ranges and affinities of other montane species occurring on the Great Plains, but which have apparently not undergone extreme speciation (or perhaps simply have not been studied). Their distributions are shown in Figures 4 - 6.

Faunal resemblance formulae (Long, 1963) were used to compare the entire faunas of each relict area in this study and the mountain ranges in Colorado and Wyoming (Johnson, 1968). Results of such comparisons agree with the general affinities indicated by the ranges of individual taxa (The Pine Ridge relates to the Black Hills first, the Bighorn Mountains second; the Black Hills relates to the Big Horn Mountains first; the Cheyenne Ridge relates to the Pine Ridge first) but were not deemed as useful in illustrating real relationships. Their values are greatly prejudiced by the unique admixtures of biota in these areas caused by the incursion of prairie biomes into the scarp woodlands, the occurrence of alpine environs only in the Black Hills and Bighorn Mountains, and the infusion of southern-related species into the river drainages of Colorado and western Nebraska.

Apparent relict populations of butterflies representing earlier vegetative events in the region were also noted in the study areas and further attest to these uniquely vegetated scarp woodlands providing refugia for species not characteristic of the surrounding plains. In the Pine Ridge, a curious *Polygonia "hylas"* (Edwards) [the name *hylas* is presently of uncertain relationship with more northern *faunus* (Edwards) but has been traditionally used for Rocky Mountain populations of the complex] or extremely green *P. progne* (Cramer) occurs in the same areas as birch relicts. Birch (*Betula* sp.) is the northern larval food-

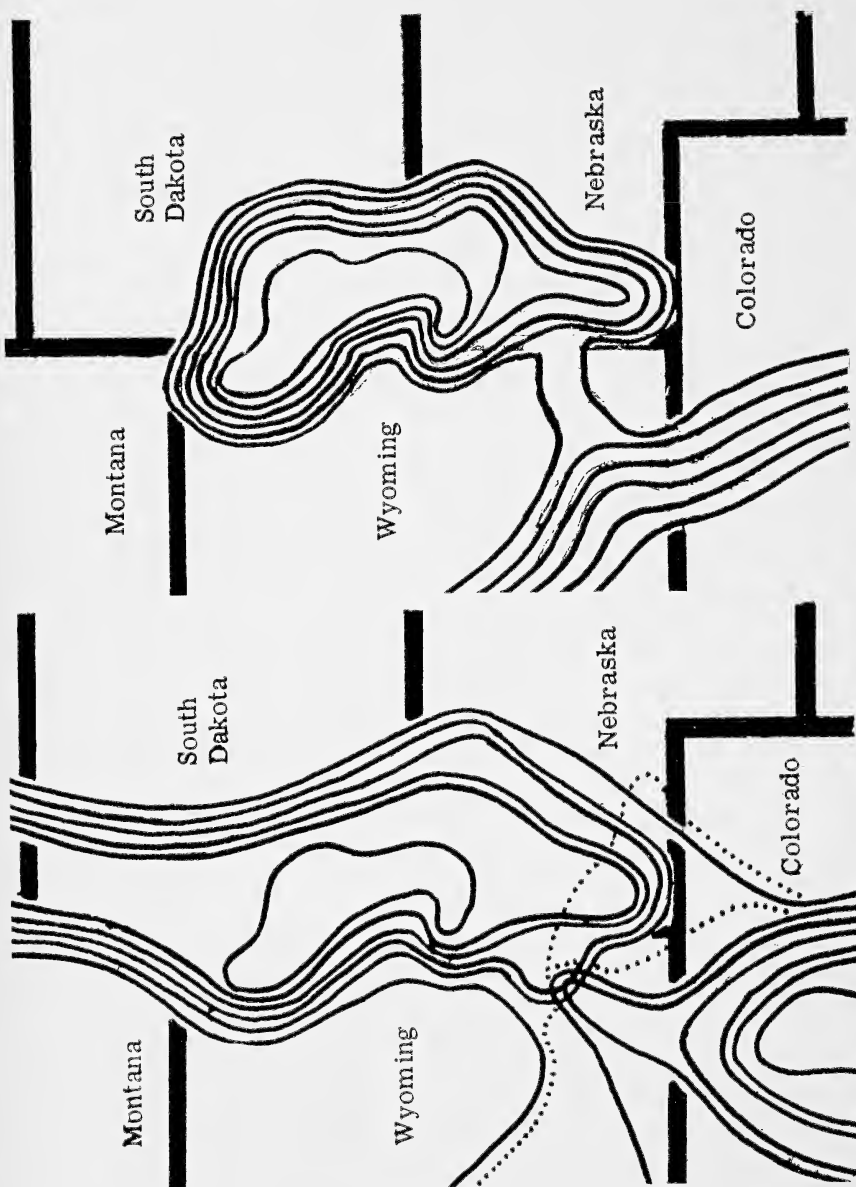


Fig. 7.—Evidence of slight secondary intergradation between *Lycaena rubidus rubidus* and *L. r. longi* in remaining populations on the plains grasslands. Each contour line represents two morphological traits in common, dotted lines one trait in common. Right: Geographic affinities of 23 male genitalic traits on 183 specimens from 62 localities. Left: Geographic affinities of 56 traits of the dorsal and ventral wing surfaces (males) on 727 specimens from 94 localities. Figure derived as a detail from Nearctic affinities in Johnson and Balogh, 1975.

plant of the *P. faunus*-*P. hylas* complex.

Also, three deciduous forest entities (*Phyciodes batesii* and *Nymphalis vaualbum j-album* of eastern origin, and *Asterocampa celtis antonia* of southern origin) occur in the river bottoms of the Pine Ridge canyons. These are relicts of the westward deciduous movement and the northward invasion of southern montane entities respectively. Most interestingly, plains river bottom populations of *A. celtis* represent the nominate subspecies *celtis* (Boisduval and LeConte) which is of eastern affinity. The uniqueness of the canyon populations was confirmed by studying and rearing the larval stages [Johnson 1972 (1973)]. Also of importance is the occurrence of an extremely allopatric and disjunctly distributed subspecies of eastern *Lethe eurydice* Johannsen along the streams in the deep escarpment canyons. This population, isolated from the formerly most western population of the species, *L. e. fumosa* Leussler, is clearly a relict of the former westward extension of the eastern deciduous forest. Unfortunately, many areas in the region highly suited for such relicts have been ill-studied by lepidopterists and our knowledge of their occurrence is limited to only those areas which have received intensive local sampling. Thus, individuals of the above species (and others) may also occur northward in the present-day disjunct conifer woodlands, as do many of the montane species mentioned earlier.

CONCLUSIONS

These data support three conclusions important to the history of butterfly speciation in the central and western Nearctic Realm.

1. The montane faunas of the remaining coniferous forests on the western Great Plains represent relicts of former, more extensive populations (not merely eastward dispersal from the mountains) and have a disjunct relationship to each other as opposed to the mountains to their west.
2. These same areas support allopatric populations of butterfly species from eastern and southern origins which are relicts of other vegetative invasions of the region.
3. This ancient montane and coniferous forest area should be considered as having formed a distinct area of speciation in the evolution of the present butterfly faunas of the Rocky Mountains and to a lesser extent those of eastern deciduous forest areas of North America.

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SPECIAL NOTES CONCERNING FORMAT
IN THIS PAPER

I have included the authors' names for each taxon on the maps in the figures.

This seemed more ideal than citing them the first time they were used in the text 1. because of the number of names in the paper 2. the fact that some are mentioned in both species or subspecies contexts at times 3. the variance in degree of study in some of these groups taxonomically.

Thus, the only authors' names mentioned in the text are in use for the first time at variance with those in the figures (e.g. when a species is discussed, but a specific trinomen is cited in the figures). Therefore, the taxonomic names in the figures form a consistent usage for the region, dependent on the degree of study each group has received by entomologists.

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(Continued from 4(3):188)

9. Deciduous Woodland (*Quercus* consociation); Plate 13.

This formation attains its greatest development on the ridges on the southern slopes of Volcán Santa Marta between elevations of 400 and 1,500 feet, i.e., above the Savanna. However, small, disjunct stands are found above the *Pinus-Quercus* Associates and on the southern slopes of Volcán San Martín Pajapan at elevations between 2,300 and 2,500 feet.

Ground cover is of variable density and consists of short grasses and sedges of which the most common are *Eragrostis* sp., *Rynchospora globosa*, *Paspalum pectinatum*, *Paspalum plicatulum*, and *Sporobolus cubensis*. *Oxalis neaei* is also common. Dense stands of *Calliandra grandiflora* and *Conostegia xalapensis* are frequent.

Quercus peduncularis, which attains a maximum height of 30 to 40 feet is the most common species of tree although *Quercus oleoides* and *Quercus ghiesbreghtii* are common. Other trees include *Byrsonima crassifolia*, *Miconia argentea*, and *Acalypha unibracteata*.

Towards the end of the dry season (mid-May), most of the oaks drop their leaves and blossom. New growth appears shortly thereafter so that the trees are not leafless for more than one or two weeks.

Epiphytes are fairly common in the taller trees, especially at elevations above 2,000 feet.

This formation appears to be a phase of the Orchard Savanna of Beard (1953) in which species of *Quercus* predominate. As stated previously, the oak forest exists principally on ridges whereas the Savanna is found on less coarse topography. Therefore, the soils within the oak forest (and which are thin, sandy, and range in color from grey to yellow) probably are more heavily leached and more efficiently drained than those in the Savanna. These two edaphic factors possibly are responsible for the existence of the Deciduous Woodland, which might be termed a modified Orchard Savanna.

10. *Pinus-Quercus* Associates; Plate 14.

The pine-oak forest is restricted to a relatively small area on the southern slopes of Volcán Santa Marta. The forest occurs on the upper slopes and crests of many of the numerous ridges between elevations of 1,600 and 3,000 feet.

Ground vegetation is of variable density and consists primarily of numerous grasses and sedges of which the most common are *Paspalum pectinatum*, *Paspalum plicatulum*, *Eragrostis*



PLATE 14

Pine-oak forest on Volcán Santa Marta near Ocotil Chico. May 1965, 1,900 feet.

sp., *Sporobolus cubensis*, *Rynchospora globosa*, *Bulbostylis papillosa*, and *Dichromena ciliata*. Other plants include *Croton repens*, *Borreria suaveolens*, *Crusea calcocephala*, *Calliandra grandiflora*, *Eupatorium incomptum*, *Calea zacatechichi*, *Ruellia fluviatilis*, *Stevia rhombifolia*, *Cordia spinescens*, *Lemourouxia viscosa*, *Conyza chilensis*, *Escobedia laevis*, *Turnera ulmifolia*, *Calea longipedicellata*, *Cassia hispidula*, *Vernonia leiocarpa*, *Salvia shannonii*, *Calea cacosmoides* (?), and *Vernonia argyropappa*. The cycad *Zamia loddigesii* is locally common.

Pinus oocarpa is the dominant tree species although *Quercus conspersa* and *Quercus ghiesbrechtii* occur rather commonly throughout the formation. Trees never form dense thickets or forests but are relatively widely distributed in open stands.

The pine-oak community represents one of the most interesting curiosities and enigmas of the Sierra de Tuxtla for the formation has such a restricted distribution. The nearest comparable formation occurs in the Department of Tuxtepec, Oaxaca, 90 miles away. The Sierra's *Pinus Quercus* community appears to be a subclimax community, which probably corresponds to the "Pine Savanna" of Beard (1953) and which is considered by that author to be a phase of the "Orchard Savanna." Beard states that pines may and usually do invade savannas when a seed source is near. However, in the Sierra pines do not occur in either the typical Savanna or the Deciduous Woodland (modified savanna), formations that exist in areas more proximal to the pine seed source in Oaxaca. Hence, additional factors probably are responsible for the limited extent of the pine-oak community. Two suggestions are offered. First, the community exists only on the crests of steep ridges, areas in which soils are extremely thin and lateritic (Friedlaender, 1923) and hence relatively poor in nutrients. Furthermore, most of the Sierra has been settled by Indians—relatively recently by Popolucas and Aztecs and formerly by Olmecs—for over 2,000 years (see Ross, 1966). Today most of the Indian villages on the Santa Marta massif are restricted to ridge crests and information gathered from Popolucan legends and stories indicates that this pattern of settlement is an ancient one. Thus the ridge crests have been subjected to severe soil disturbances for at least hundreds of years. Numerous works, e.g., those of Pessin (1937), Stoaite (1950), and Merrifield, Foil, and Hansbrough (1964), have shown that pines can grow well in soils with relatively low concentrations of nutrients and which are too poor for many



PLATE 15
Littoral Woodland near Zapopan; view is towards the southeast. May 1965,
sea level.

plant species. Therefore, I conclude that the ridge crests represent a favorable habitat for pines and a relatively unfavorable one for many (or even most) other species of trees. Second, the Popolucas today engage (and have engaged for hundreds of years) in annual burnings of the pine lands. These burnings significantly increase the geographic extent of the pine-oak community for whenever fire is excluded from an area for several consecutive years a heavy ground cover consisting of numerous grasses, shrubs, and oak saplings develops. These saplings develop later into trees; pine seedlings usually are never present (Ross, 1966). Therefore, I conclude that the pine-oak community in the Santa Marta area is a seral stage within the Deciduous Woodland (which in turn is a modified savanna) and which has become established because of favorable edaphic conditions and is being maintained in its present extent by man-caused fires.

The ravines within the *Pinus-Quercus* Associates contain elements of the Semi-Evergreen Seasonal Forest.

DRY EVERGREEN FORMATION

11. Littoral Woodland or Dry Evergreen Woodland (*Ficus-Hibiscus* Association); Plate 15.

This formation occurs along the seashore between the high water mark and the volcanic headlands fronting the Gulf. Hence the formation is variable in width, extending inland for only a few feet or to 500 to 1,000 feet. Strong winds and salt spray are common throughout.

Along the sandy beaches the following plant species are common: *Cyperus ligularis*, *Cyperus articulatus*, *Cenchrus incertus*, *Distichlis spicata* or *Sporobolus virginicus*, *Chloris petraea*, *Vigna luteola*, *Ipomoea stolonifera*, and *Ipomoea pes-caprae*.

Farther inland are small, gnarled, and windswept trees and shrubs, which are found both in small open patches and in extensive dense thickets. These woody species include *Ficus* spp., *Hibiscus titiaceous*, *Pachira aquatica*, and *Piper cordovan*.

SWAMP FORMATIONS

12. Swamp Forest (*Pachira-Ficus* Association); Plate 16.

The Swamp Forest is located at low elevations near the Gulf and bordering several of the large streams, e.g., Río Zapoa-



PLATE 16
Swamp Forest near Zapopan. May 1965, sea level.

pan, Río Carizal, Río Salado, Río Yougualtajapan, and Río Máquina. The ground in this formation is waterlogged during most of the year and is frequently inundated for long periods during the rainy season.

The understory is relatively open and is composed principally of *Chamaedorea tepejilote*, *Piper cordovan*, and numerous saplings.

The single tree stratum ranges between 40 and 60 feet in height and is composed principally of *Pachira aquatica*, *Ficus* spp. (including *Ficus obtusifolia*), *Hibiscus tiliaceus*, and *Pleuranthodendron mexicana*.

Many trees exhibit buttressing and stiltling. Lianas and epiphytes are common.

13. Mangrove Woodland (*Rhizophora* consociation); Plate 17.

This formation is restricted to the margins of Bahía Sontecomapan. *Rhizophora mangle* is the only principal species and forms thick, closed stands up to 40 or 60 feet in height. Stilt roots and pneumatophores are common.

UNRESTRICTED MISCELLANEOUS FORMATIONS

14. Recently Abandoned Milpas; Plate 18.

When a milpa or corn field is abandoned the field is invaded by numerous grasses and annuals. The latter include *Melampodium divaricatum* and *Ageratum conyzoides*, both of which blossom in the spring and which are replaced in the summer by *Baltimora recta*, *Bidens pilosa* var. *bimucronata*, and *Melampodium kunthianum*. In subsequent years these species usually are replaced by more woody plants such as *Polymnia maculata*, *Cordia spinescens*, *Hamelia patens*, *Piper auritum*, *Conostegia xalapensis* (Andrle, 1964), *Heliotropium indicum*, *Calliandra grandiflora*, and *Vernonia leiocarpa*.

15. Pastures; Plate 19.

Areas that are used consistently for the grazing of cattle and/or horses usually develop rather distinctive floristic characteristics. There are numerous patches or clumps of relatively short vegetation composed of *Cordia alliodora*, *Croton soliman*, *Picramnia andicola*, *Heliotropium indicum*, *Crotalaria vitellina*, *Urera elata*, *Solanum ochraceo-ferrugineum*, and *Piper auritum*. Trees, which are relatively few in number, include *Inga spuria*, *Inga leptoloba*, *Cassia spectabilis*, *Cassia occidentalis*, *Annona reticulata*, *Annona muricata*, *Trema micrantha*, and *Pleuranthodendron mexicana*.



PLATE 17
Mangrove Woodland along
Bahia Sontecomapan. May 1962, sea level.
Photograph by R. F. Andrie.

16. Hedgerows; Plate 20.

Corn fields and pastures in the more heavily cultivated sections of the Sierra, e.g., in the vicinity of the larger cities and towns, usually are bordered by fences about which is found a varied but characteristic assemblage of plants. Where best developed these rows may be as wide as 15 to 20 feet. The undergrowth usually is a tangle of vegetation composed of *Cordia spinescens*, *Urera elata*, *Passiflora serratifolia*, and *Passiflora coriacea*. Tree species attain maximum heights of 20 to 30 feet and include *Bursera simaruba*, *Gliricidia sepium*, *Erythrina americana* (Andrle, 1964), *Zanthoxylum elephantiasis*, *Ficus padifolia*, *Inga spuria*, *Inga leptoloba*, *Cassia spectabilis*, *Annona muricata*, and *Annona reticulata*.

V. ACCOUNTS OF BUTTERFLY SPECIES IN
THE SIERRA DE TUXTLA
Plan of the Species Accounts

Unfortunately, systematics of the Lepidoptera, especially tropical forms, is in a relatively unstable state. Indeed, between one-third and one-half of the species listed in the "Catalogo Sistemático y Zoogeográfico de los Lepidópteros Mexicanos" (Hoffmann, 1940) do not bear today the same generic and specific names. For this reason I have had to rely on numerous and isolated taxonomic works in addition to personal correspondence in order to present here a reasonably accurate and modern systematic arrangement of taxons. In particular, I have followed Munroe and Ehrlich (1960) for the arrangement of the Papilionidae, Klots (1931) for the Pieridae, Fox (1956) for the Ithomiidae, Michener (1942) and Emsley (1963) for the Heliconiinae (Nymphalidae), Forbes (1944) and Higgins (1960) for the Argyninidi (Nymphalidae), Chermock (1950) for the Liminitidi (Nymphalidae), and Clench (1955) for the Lycaenidae and Riodinidae. Thus, it is hoped that this paper, although not intended to be taxonomically oriented, nevertheless will represent a significant contribution to the systematic literature and serve as a modern reference for students of Neotropical Lepidoptera.

Each species account is introduced by the scientific name of the species. Following this heading and under the caption



PLATE 18

Recently Abandoned Milpa on Volcán San Martín Tuxtla. Field has remained fallow for approximately one year. June 1962, 2,350 feet. Photograph by R. F. Andrade.

SPECIMEN or SPECIMENS are the field data. For those species that previously have been recorded from the Sierra, the data have been condensed and include number of specimens of each sex, maximum-minimum altitudes (elevations were measured with a Taylor "Forecaster-Altimeter" calibrated to measure in 200 foot intervals), and earliest-latest collection dates. For those species that represent new records for the Sierra or which are rare, the complete field data are given (mileages represent straight-line distances). If a particular specimen is in a collection other than my own, initials of the collection are included. The following initials are employed: KHW = personal collection of Kent H. Wilson and LSUMZ = Louisiana State University Museum of Zoology. Sequence of entries is determined primarily by altitude (lowest elevation listed first) and secondarily by collection date (the earliest day and month listed first). Thus, the first and last entries give the altitudinal range of the species.

Following the data is a discussion paragraph. In the first sentence I express the relative abundance of the species in the Sierra by employing four general terms—abundant, common, uncommon, and rare. I consider a species to be abundant if ten or more individuals of it were noted every (or almost every) day, common when less than ten individuals were noted each day, and uncommon when only three to five individuals were seen at fairly wide intervals of time. Those species collected only after very long time lapses or only once or twice during my residence are designated as rare. Unfortunately, these terms are extremely difficult to standardize when referring to animals in the tropics because of the overwhelming array of inconspicuous and virtually uncollectible habitats. Therefore, in many cases the evaluation of the relative abundance of a species may be very biased and not reflect the actual status of the species. In the second sentence (and frequently in the latter part of the first) I give the principal plant formation or formations inhabited by the species. Sequence of formations is based on decreasing relative abundance of the butterfly species. The remaining sentences are devoted to general comments, principally on the ecology and ethology of the species, that I consider pertinent. When a species previously has not been recorded from the Sierra, the nearest recorded locale is given in the last sentence of the paragraph.



PLATE 19
Pasture near Zapoapan. May 1965, sea level.

Accounts
FAMILY PAPILIONIDAE
SUBFAMILY Papilioninae

TRIBE Graphiini

SUBTRIBE Graphiiti

1. *Graphium phaon* (Boisduval)

SPECIMENS: 10 ♂♂, 1 ♀; 1,100-1,800 feet; 12 May-3 Oct.

This species is common along hedgerows, particularly in the vicinity of Lago Catemaca. Most butterflies were collected as they imbibed moisture from wet sand and soil. The flight is relatively rapid, erratic, and usually between two and four feet of the ground. Two of the 11 specimens collected exhibit a loss of marginal and submarginal greenish dots on the dorsal fore wings and a replacement of the postmedian-median row of greenish scales on the dorsal hind wings with red scales. This morphotype, which has been named form *eridamas* (Reakirt), bears a close resemblance to *Parides polyzelus* (Papilioninae: Troidini), a species that is abundant along hedgerows and the margins of forests.

2. *Graphium branchus* (Doubleday)

SPECIMENS: 3 ♂♂; 2 mi. NE Catemaco, 1,100 feet, 27 July 1962, 1 ♂; 3 Aug. 1962, 1 ♂: Ocotal Grande, 1,800 feet, 15 May 1965, 1 ♂.

This tailless *Graphium* is uncommon and was collected along the margins of the Semi-Evergreen Seasonal Forest only in late spring and summer. The flight is relatively close to the ground (usually within three or four feet) and similar in velocity to that of *Parides* spp. This species was recorded previously from Veracruz only from the "Sierra Madre Oriental" (Hoffmann, 1940).

3. *Graphium belesis* (Bates)

SPECIMENS: 18 ♂♂, 6 ♀♀; 1.5 mi. SSE Sontecomapan, 900 feet, 14 July 1962, 1 ♀; 2 mi. NE Catemaco, 1,100 feet, 1 July 1963, 1 ♂; 2 July 1962, 1 ♀; 9 July 1962, 1 ♀ (KHW); 27 July 1962, 2 ♂♂ (1 KHW); 9 Aug. 1962, 1 ♂; 31 Aug. 1962, 1 ♂;



PLATE 20

Hedgerow near San Andrés Tuxtla. Although the predominant tree in the photograph is *Bursera sinarubra*, numerous other species of trees and shrubs usually are present. June 1962, 1,300 feet. Photograph by R. F. Andrie.

8 Sept. 1962, 1 ♀ : 4.5 mi. NE Catemaco, 1,100 feet, 26 June 1962, 1 ♂ : 4 mi. S Coyame, 1,200 feet, 25 June 1962, 3 ♂ ♂ : 2.5 mi. SW Sontecomapan, 1,300 feet, 26 June 1962, 1 ♂ : 1 mi. N So-teapan, 1,400 feet, 28 March 1965, 1 ♂ ; 29 March 1965, 2 ♂ ♂ : 1 mi. SSW Vigía, 1,800 feet, 18 March 1965, 1 ♀ : 1 mi. NNE Ocotál Chico, 2,000 feet, 1 ♂ , 1 ♀ : 2 mi. NNW Ocotál Chico, 3,800 feet, 1 ♂ . Reared specimens: 2 mi. NE Catemaco, 1,100 feet, emerged 30 July 1962, 1 ♂ (KHW); emerged 3 Sept. 1962, 1 ♂ ; emerged 6 Sept. 1962, 1 ♂ .

This species is abundant during the spring and summer months along the margins of the Semi-Evergreen Seasonal Forest and Hedgerows, particularly in the vicinity of Lago Catemaco. Adults are attracted to wet sand and soil. The flight is usually slow and within three feet of the ground, a behavior that is atypical for most members of the genus. Of the 24 specimens collected, two have faint white blotches on their dorsal fore wings. This morphotype, named form *hephaestion* (Felder), bears a close resemblance to females of *Parides* spp. Larvae (described in Ross, 1964b) were found occasionally on *Annona muricata*, a tree called "Guanabana" by the local residents and commonly planted around habitations. *G. belesis* was recorded previously from Veracruz only from the "Sierra Madre Oriental" (Hoffmann, 1940).

4. *Graphium philolaus* (Boisduval)

SPECIMENS: 3 ♂ ♂ , 1 ♀ ; 1,100-1,200 feet; 20, 27 June.

Although only four specimens were taken, the species is common during the spring and early summer months, in pastures and along sunny road sides in the vicinity of Lago Catemaco. The butterflies are attracted to moist earth and to the flowers of *Inga leptoloba*, a tree common in pastures. *G. philolaus* exhibits the high, soaring flight that is characteristic of most species in the genus.

5. *Graphium epidaus epidaus* (Doubleday, Westwood, & Hewitson)

SPECIMENS: 11 ♂ ♂ , 3 ♀ ♀ ; 1,100 feet; 20 June-27 July.

Adults are very abundant during the spring and summer months in Pastures, Recently Abandoned Milpas, and along Hedgerows and sunny road sides throughout the Sierra but particularly in the vicinity of Lago Catemaco. This distribution correlates with the distribution of the larval food plant *Annona reticulata*, a tree that produces sweet fruit and which is cultivated frequently by the local inhabitants. Adults exhibit the

characteristic *Graphium* flight and are attracted to mud puddles and damp soil and sand. Immature stages (described in Ross, 1964b) were found commonly on the leaves of the food plant during the summer months.

6. *Graphium agesilaus neosilaus* (Hoffer)

SPECIMENS: 4 ♂♂; 2 mi. NE Catemaco, 1,100 feet, 2 July 1962, 2 ♂♂: 1 mi. N Soteapan, 1,400 feet, 28 March 1965, 2 ♂♂.

This "kite swallowtail" is uncommon and was collected only along sunny road sides during spring and early summer. All four specimens were taken as they drank from damp sand. The previous Veracruz record is the "Sierra Madre Oriental" (Hoffmann, 1940).

7. *Graphium calliste calliste* (Bates)

SPECIMENS: 16 ♂♂, 1 ♀; 4,100-5,100 feet; 3 March-7 April.

G. c. calliste is abundant above the canopies of the Montane Thicket and Elfin Woodland during March and April. The butterflies descend to within a few feet of the ground usually only to visit flowers, particularly those of *Schistocarpha* sp. (a composite that is common on the open, sunny ridges and crater walls).

TRIBE Troidini

SUBTRIBE Battiti

8. *Battus polydamas* (Linnaeus)

SPECIMENS: 6 ♂♂, 4 ♀♀; 0-2,700 feet; 10 March-14 Aug.

B. polydamas is abundant in the Littoral Woodland and common in all other formations except the Montane series. Adults are attracted to the flowers of *Lantana camara* and to moist soil and sand. The flight is relatively rapid and usually within eight feet of the ground. When pinched, specimens protruded their yellowish abdominal scent glands, which emitted an acrid odor. Larvae were found on *Aristolochia asclepiadifolia*, a vine that is common in the vicinity of the Popoluca Indian villages on the Santa Marta massif.

9. *Battus belus varus* (Kollar)

SPECIMENS: 4 ♀♀; 700-1,400 feet; 20 May-14 July.

This papilionid is locally common, being seen most frequently along the margins of the Semi-Evergreen Seasonal Forest in the ravines within the oak and pine-oak forests. The flight usually is above ten feet of the ground. Two of the four specimens were taken as they fed on the blossoms of *Inga spuria*. The abdominal scent glands produce an acrid odor.

10. *Battus laodamas copanae* (Reakirt)

SPECIMENS: 1 ♂, 1 ♀; 2 mi. NE Catemaco, 1,100 feet, 24 June 1962, 1 ♀; 28 June 1962, 1 ♂.

This rare species was collected only in Pastures; the female as it fed on the blossoms of *Lantana camara* and the male as it flew about the blossoms of *Inga spuria*. The flight is relatively rapid and erratic.

SUBTRIBE Troiditi

11. *Parides photinus* (Doubleday)

SPECIMENS: 8 ♂♂, 5 ♀♀; 700-5,100 feet; 30 March-30 Aug.

This species is common in all the Montane Formations and the Semi-Evergreen Seasonal Forest on the Santa Marta massif. The butterflies are particularly numerous along sunny trails and in bright glades with the forests. The flight is relatively slow and usually within four feet of the ground. However, when individuals are disturbed they fly rapidly with powerful wing beats. The abdominal scent glands emitted an acrid odor when the butterflies were pinched. The larval food plant is *Aristolochia asclepiadifolia*, the same as that of *Battus polydamas*. Immature stages are described elsewhere (Ross, 1964d).

12. *Parides montezuma* (Westwood)

SPECIMENS: 4 ♂♂; 1,050-2,000 feet; 1 Aug.-29 Oct.

This tailed *Parides* is locally common, being found most frequently in the Recently Abandoned Milpas surrounding the Indian villages of Mecayapan and San Fernando. The butterflies fly fairly rapidly between four and ten feet of the ground and are attracted to flowers. The abdominal scent glands produce an acrid odor.

13. *Parides polyzelus polyzelus* (Felder)

SPECIMENS: 21 ♂♂, 6 ♀♀; 0-1,900 feet; 13 March-5 Oct.

This papilionid is abundant in the Semi-Evergreen Seasonal Forest, Lower Montane Rain Forest, Littoral Woodland, Swamp Forest, and along Hedgerows. In fact, this species is the most common forest-inhabiting swallowtail. The flight is relatively slow, weak, and usually within three or four feet of the ground. The abdominal scent glands produce acrid odors.

14. *Parides sesostris zestos* (Gray)

SPECIMENS: 4 ♂♂, 1 ♀; 0-1,750 feet; 12 July-29 Oct.

This swallowtail is locally common, being found in the Lower Montane Rain Forest, Semi-Evergreen Seasonal Forest, Littoral

Woodland, and Swamp Forest. It and the following two species, *P. iphidamas* and *P. arcas mylotes*, in addition to being very similar in appearance, seem to be very closely related ecologically and ethologically. For example, all three species prefer the relatively bright or sunlit sections of mature forests below an elevation of approximately 3,000 feet and usually are found in localized assemblages. The flight is rapid and within three to five feet of the ground. As reported in Ross (1964a), the butterflies appear to have definite "flyways" from which they very rarely deviate. These flyways usually are sections of relatively wide trails. The abdominal scent glands produce an acrid odor.

15. *Parides iphidamas* (Fabricius)

SPECIMENS: 16 ♂♂, 9 ♀♀; 0-2,450 feet; 13 March-18 Oct.

This species is locally common (more common than *P. sesostris zestos*) in the Lower Montane Rain Forest, Semi-Evergreen Seasonal Forest, Littoral Woodland, and Swamp Forest. The flight behavior is the same as that of *P. sesostris zestos*. The abdominal scent glands, as those of other members of the genus, produce an acrid odor.

16. *Parides arcas mylotes* (Bates)

SPECIMENS: 17 ♂♂, 13 ♀♀; 0-2,700 feet; 13 March-24 Oct.

P. arcas mylotes is locally abundant in the Lower Montane Rain Forest, Semi-Evergreen Seasonal Forest, Littoral Woodland, and Swamp Forest. The flight behavior is the same as that described under *P. sesostris zestos*. The abdominal scent glands emit an acrid odor.

TRIBE Papilionini

17. *Papilio polyxenes asterius* Stoll

SPECIMENS: 3 ♂♂, 2 ♀♀; 1,100-2,700 feet; 5 May-14 Sept.

This "fluted swallowtail" is uncommon and was collected only in the *Pinus-Quercus* Associates of the Deciduous Woodland and in a small, disjunct patch of oak forest NNE of Catemaco. Two of the five specimens are typical *P. polyxenes asterius* whereas the remaining three are of the morphotype named form *americus* Kollar. The flight is characteristic of most members of the genus *Papilio*—rather rapid with strong wing beats and usually between six and 15 feet of the ground.

18. *Papilio thoas autocles* Rothschild & Jordan

SPECIMENS: 12 ♂♂, 5 ♀♀; 0-2,700 feet; 12 March-30 Sept.

This species is the most common swallowtail in the Sierra and occurs in Recently Abandoned Milpas, Pastures, Semi-Evergreen Seasonal Forest, Littoral Woodland, and along Hedgerows and

most sunny road sides. The butterflies visit the blossoms of numerous species of plants and mud puddles. The flight is typical of *Papilio* spp. Larvae, described in Ross (1964d) were found on *Piper marginatum* and *Piper kerberi*, both of which are common along shaded stream banks in the Semi-Evergreen Seasonal Forest on the Santa Marta massif.

19. *Papilio androgeus epidaurus* Godman & Salvin

SPECIMENS: 7 ♂♂, 1 ♀; 1,100-5,100 feet; 24 March-13 Oct.

This papilionid is common above the canopy of the Elfin Woodland. Most butterflies were collected as they flew in circular patterns between eight and 12 feet above the peaks of Cerro Tuxtla and Volcán Santa Marta. This behavior is commonly known as "hilltopping." Larvae (described in Ross, 1964b) were found during the summer months on *Zanthoxylum elephantiasis*, a small tree that is common in the hedgerows bordering Lago Catemaco.

20. *Papilio anchisiades idaeus* Fabricius

SPECIMENS: 6 ♂♂, 8 ♀♀; 500-1,800 feet; 20 June-9 Oct.

This swallowtail is common in Pastures and along Hedgerows in the vicinity of Lago Catemaco and most towns and villages throughout the Sierra where citrus trees are cultivated, *Citrus* spp. being the larval food plant. The flight is typical of most species in the genus. Immature stages are described in Ross (1964b).

21. *Papilio victorinus victorinus* Doubleday

SPECIMENS: 1 ♂, 1 ♀; 2 mi. NE Catemaco, 1,100 feet, 28 July 1962, 1 ♂; 2.5 mi. NNW Ocotil Chico, 3,000 feet, 12 April 1965, 1 ♀.

This species is rare; the male was collected in a sunny glade within the Semi-Evergreen Seasonal Forest and the female along a wide logging road in the Montane Rain Forest. Both specimens were flying rapidly approximately ten to 12 feet above the ground when collected.

FAMILY PIERIDAE
SUBFAMILY Dismorphiinae

22. *Dismorphia (Dismorphia) praxinoe* (Doubleday)

SPECIMENS: 8 ♂♂, 12 ♀♀; 0-4,300 feet; 13 March-17 Nov.

D. praxinoe is locally common, being found principally in the Lower Montane Rain Forest, Montane Rain Forest, Semi-Evergreen Seasonal Forest, and Swamp Forest. The flight is very weak and the butterflies very rarely rise more than four feet above the forest floor. As reported previously (Ross, 1964a), this slow, weak flight is very atypical for members of the Pieridae but very similar to that of many species in the family Ithomiidae.

23. *Dismorphia (Dismorphia) fortunata* (Lucas)

SPECIMENS: 34 ♂♂, 19 ♀♀; 700-5,000 feet; 9 Feb.-30 Oct.

This species locally abundant and found principally in the Lower Montane Rain Forest, Montane Rain Forest, Semi-Evergreen Seasonal Forest, and Swamp Forest. The flight is weak and slow, much more so than that of the related species *D. praxinoe*. The butterflies usually fly within one to two feet of the forest floor. This flight behavior is very similar to that of several species of ithomiids, principally *Oleria paula*, *Pteronymia cotyto*, and *Hypoleria cassotis* (see Ross, 1964a also).

24. *Dismorphia (Dismorphia) euryope* (Lucas)

SPECIMENS: 11 ♂♂, 1 ♀; 3 mi. NNW Ocotil Chico, 4,100 feet, 23 Feb. 1965, 1 ♂; 12 March 1965, 1 ♀; 4,300 feet, 7 March 1965, 1 ♂; 4,400 feet, 17 June 1963, 1 ♂; 30 July 1963, 3 ♂♂; 4,800 feet, 5 April 1965, 1 ♂; 16 July 1963, 2 ♂♂: Peak Volcán Santa Marta, 5,000 feet, 11 June 1963, 1 ♂; 5,100 feet, 26 May 1965, 1 ♂.

This pierid is local and uncommon; all specimens were collected in the Montane Thicket and Elfin Woodland on Volcán Santa Marta. The flight, particularly that of the males, is more rapid and erratic than that of the preceding two species but still slower than that of most pierids. The butterflies were collected most frequently as they rested on leaves in relatively bright or sunny glades within the forests. The body fluids of pinched specimens smelled sour. The previous Veracruz record is the "Sierra Madre Oriental" (Hoffmann, 1940).

(to be continued)

NOTICES

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INDEXES: Index to volume 11 is in volume 13, no. 3, to volume 12 is in volume 13, no. 1.

PUBLICATIONS: The Swallowtail Butterflies of North America. Hamilton A. Tyler, Naturegraph Publishers Inc. Healdsburg, Calif. 95448. Paper \$5.95, cloth \$9.95.

Mites of Moths and Butterflies. Asher E. Treat, Cornell Univ. Press, 124 Roberts Place, Ithaca, N. Y. 14850. \$35.00

Geographical Variability in Speyeria. Arthur H. Moeck, reprint. Entomological Reprint Specialists, P. O. Box 77224, Dockweiler Sta., Los Angeles, CA 90007.

Butterflies of Lebanon. Torben B. Larsen, Nat'l Council for Sci. Res., Republic of Lebanon. Avail. in U. S. A. from E. R. S. (see above) \$22.50.

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Volume 14

Number 4

December, 1975

IN THIS ISSUE

A revision of

the North American *Comadia*

(Cossidae)

Richard M. Brown

189

A note on *Oeneis Melissa* (Fabricius)

in the western United States (Satyridae)

Clifford D. Ferris

213

Post Pleistocene environments and

montane butterfly relicts

on the western great plains

Kurt Johnson

216

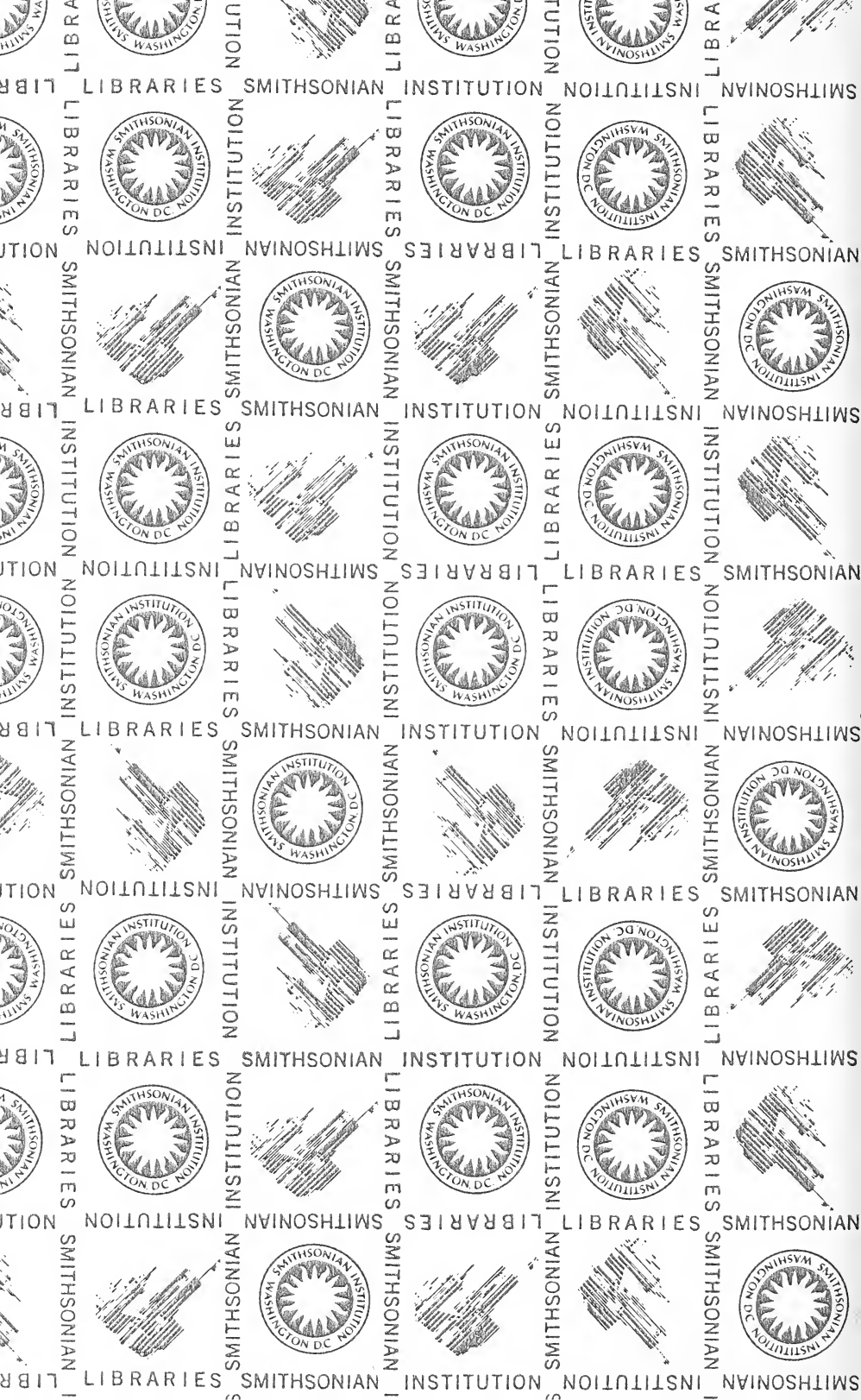
An ecological study of the butterflies of

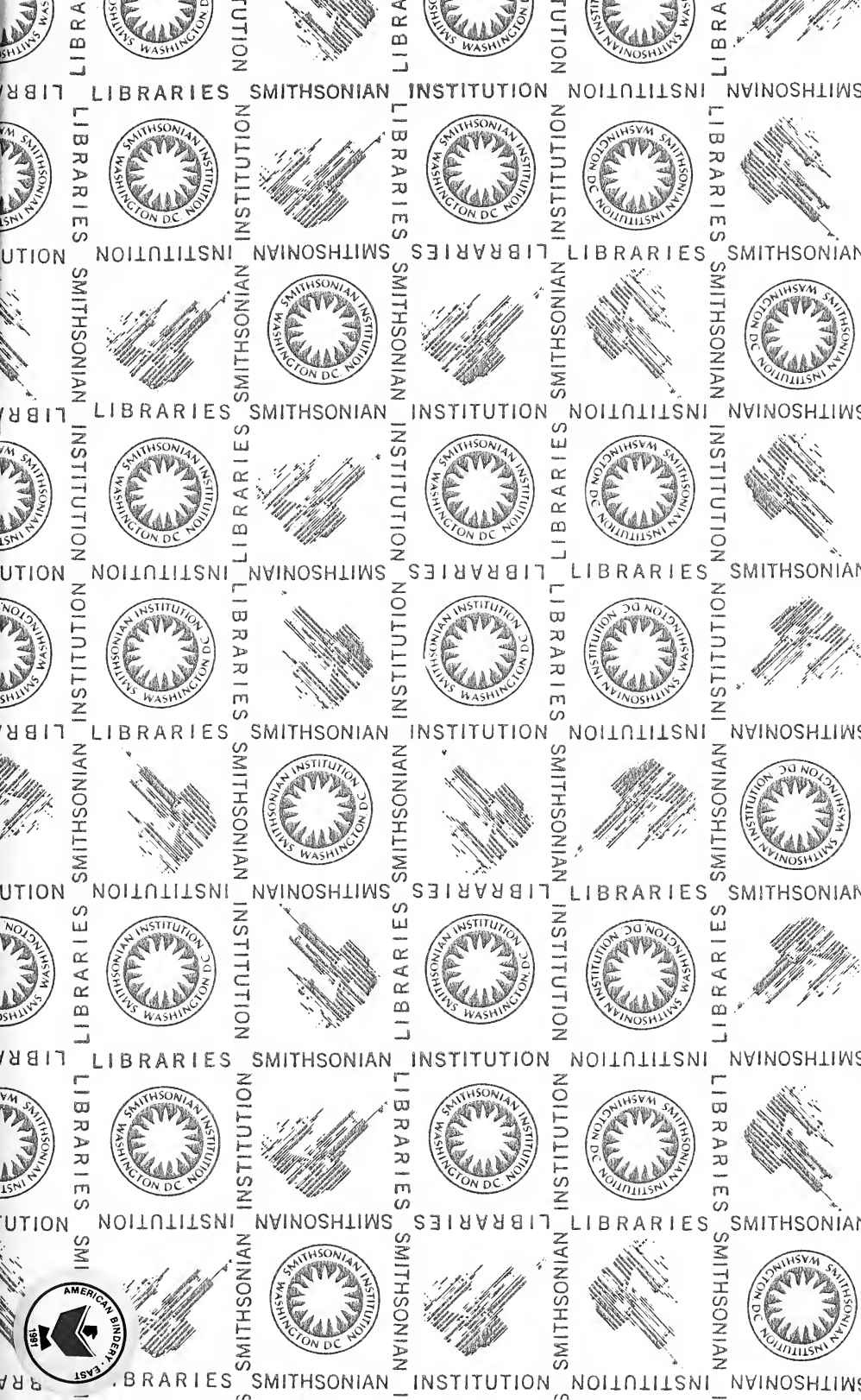
the Sierra de Tuxtla in Veracruz, Mexico

Gary N. Ross

233







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